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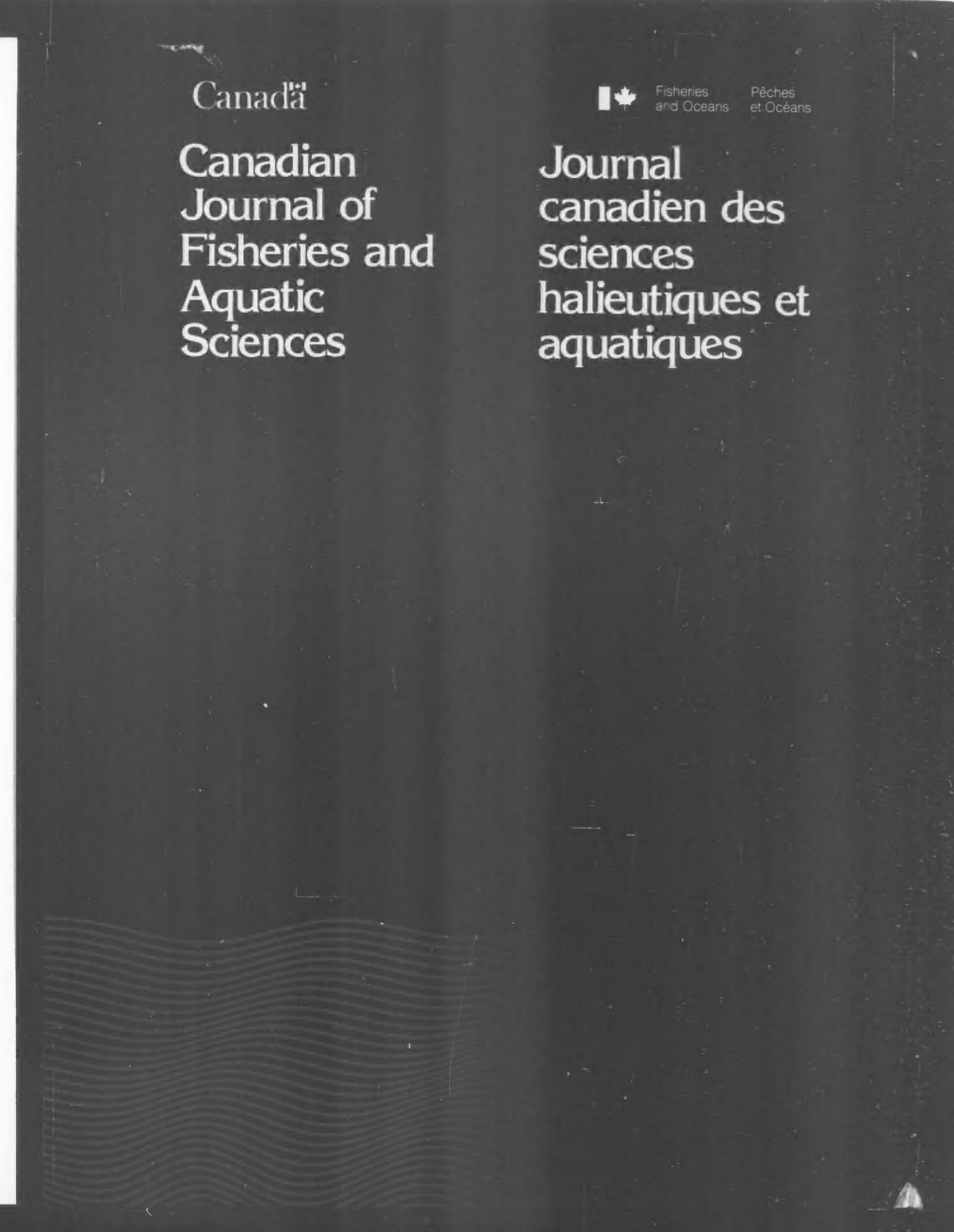

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Quantitative Estimation of Epiphytic Invertebrate Populations[1]

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Downing, J. A., and H. Cyr. 1985. Quantitative estimation of epiphytic invertebrate populations. Can. J. Fish. Aquat. Sci. 42: 1570–1579.

Quantitative comparisons were made of the relative accuracy, precision, and cost of various population estimation techniques for epiphytic invertebrates. Quadrat clipping was often more accurate than the Gerking, Macan, Minto, or KUG samplers, yielding population estimates an average of sevenfold greater where differences were found. All quadrat sizes (112 cm^2 to 1 m^2) usually yielded equal estimates of epiphytic invertebrate populations. The spatial variance of replicate epiphytic invertebrate samples increased with population density and decreased with the size of sampler employed ($R^2 = 0.94$; $n = 497$). All samplers yielded equivalent levels of sampling precision. A method providing provisional estimates of the requisite number of replicate samples for a given level of precision is presented. Greater replication is required at low invertebrate population density or when small samplers are used. The most cost effective sampler size for the phytofauna is about 500 cm^2. Improved sampling design can result in up to fivefold reductions in sampling effort. Taxa examined include Acari, Amphipoda, Chironomidae, Cladocera, Copepoda, Gastropoda, Hirudinea, Lepidoptera, Nematoda, Oligochaeta, Ostracoda, Trichoptera, and Turbellaria.

Les auteurs ont effectué des comparaisons quantitatives de la précision, de l'exactitude et du coût relatifs de diverses techniques d'estimation démographique d'invertébrés épiphytes. L'échantillonage par quadrat s'est souvent révélé plus précis que les échantillonneurs Gerking, Macan, Minto ou KUG; en moyenne, cet échantillonnage fournissait des estimations démographiques sept fois plus élevées quand des différences étaient présentes. Toutes les tailles de quadrat (de 112 cm^2 à 1 m^2) ont généralement donné des estimations équivalentes des populations d'invertébrés épiphytes. La variance spatiale des échantillons répétés d'invertébrés épiphytes augmentait en fonction de la densité de la population et diminuait en fonction de la taille de l'échantillonneur utilisé ($R^2 = 0{,}94$; $n = 497$). Les auteurs ont obtenu des taux équivalents de précision d'échantillonnage avec tous les échantillonneurs. Ils présentent une méthode d'estimation provisoire du nombre d'échantillons répétés nécessaire à l'obtention d'un niveau donné de précision. Un plus grand nombre d'échantillons répétés est nécessaire quand la densité des invertébrés est faible ou que de petits échantillonneurs sont utilisés. Pour la phytofaune, l'échantillonneur le plus rentable est celui qui mesure environ 500 cm^2. Une conception améliorée de l'échantillonnage peut permettre de diminuer l'effort d'échantillonnage d'un facteur allant jusqu'à cinq fois. Les taxons étudiés sont les suivants : Acari, Amphipoda, Chironomidae, Cladocera, Copepoda, Gastropoda, Hirudinea, Lepidoptera, Nematoda, Oligochaeta, Ostracoda, Trichoptera et Turbellaria.

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The invertebrates living on the surfaces of aquatic macrophytes are important in freshwaters because they are very abundant (Pieczyńska 1973), highly productive (Guziur et al. 1975; Howard-Williams and Lenton 1975), and constitute a major source of food for forage- and sport-fish (Bigelow 1923, 1928; Gascon and Leggett 1977; Hall and Werner 1977; Keast and Harker 1977; Keast 1978; Werner et al. 1978; George and Hadley 1979; Laughlin and Werner 1980; Baltz and Moyle 1982; Fairchild 1982). In spite of this importance, the high cost and variability of invertebrate population estimates have led to a paucity of conclusive studies of their production, population ecology, or community dynamics (Pieczyńska 1973; Downing 1984). Kajak (1971) suggested that studies of the reliability of estimates obtained using various techniques would be necessary before quantitative results could be relied upon. Comparisons of the relative accuracy, bias, and precision of phytofauna population estimation techniques are still lacking (Downing 1984).

Most methods for estimating the abundance of epiphytic invertebrates isolate a set area of the lake bottom from which macrophytes and attached invertebrates are collected. Macrophytes are often enclosed in quadrat frames (400 cm^2 to 1 m^2), and the plants are clipped at the base and collected in plastic (Soszka 1975; Mackey 1976) or mesh (e.g. DeCoster and Persoone 1970; Calow 1973) bags. Such quadrat clipping risks the loss of invertebrates upon collection; thus, special samplers have been designed that enclose macrophytes and animals before macrophytes are cut. These include the box samplers of Gerking (1957; Fig. 1A), Macan (1949; Fig. 1B), and Minto (1977; Fig. 1C). These samplers are pushed into the vegetation, the macrophytes are cut either by closure or by hand, and the sample is retrieved and backwashed into a container. The KUG sampler is a more complex remote, grab-like, closing mesh-bag sampler (Shapovalova and Vologdin 1979; Fig. 1D). The sampler frame is dropped so that the bag encloses the macrophytes. Upon closure, the macrophyte stems are cut above the

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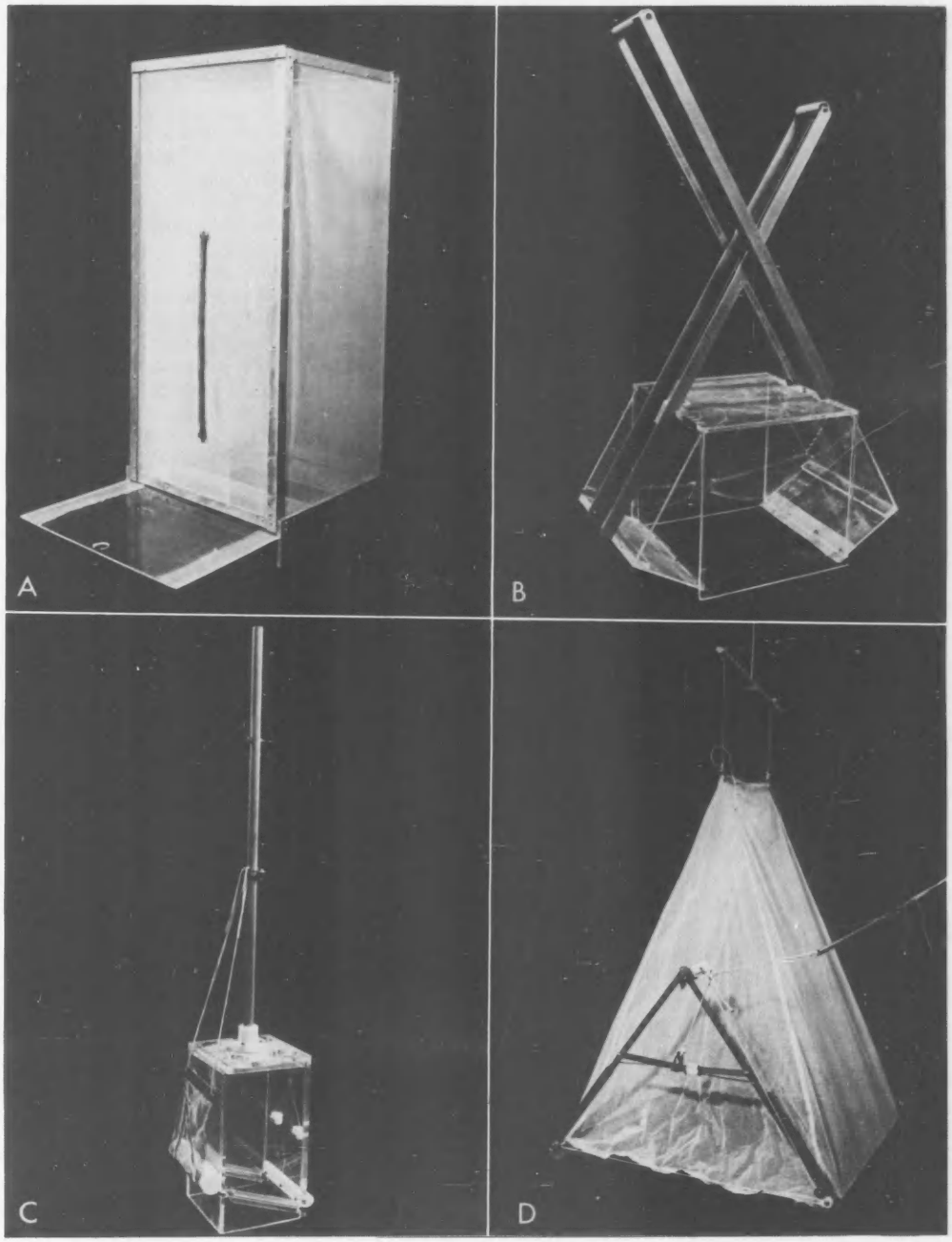

FIG. 1. Samplers used for comparisons in this study. Some minor modifications were made over the original designs. The door of the Gerking sampler (A) was made of transparent plastic sheet instead of screen-covered metal, the copper screen sides were replaced with 100-μm nylon mesh, the height was increased to 1.2 m to permit deeper sampling, and one side was fitted with a large Delrin™ zipper to facilitate cutting of macrophytes. The bodies of the Macan sampler (B) and the Minto sampler (C) were made of transparent plastic. The conical net of the KUG sampler (D) was made of 100-μm nylon net and the apex was fitted with a large zipper. All seams were felled and zippers were covered with protective mesh flaps. Construction of solid parts was of aluminum and stainless steel (Gerking and Macan), aluminum, stainless steel, and machined Teflon™ (Minto), and brass, stainless steel, and machined Teflon™ (KUG). Sampler sizes were 1793 cm^2 (Gerking), 815 cm^2 (Macan), 189 cm^2 (Minto), and 4724 cm^2 (KUG). All modifications were made to decrease sampler avoidance and increase sample retention. Photographs courtesy of Jean-Luc Verville, Université de Montréal.

sediment surface. Many other phytofauna samplers have been described (Downing 1984 for review) but quadrat sampling and the Gerking, Macan, Minto, and KUG samplers are among the most frequently cited and include the major sampler concepts in use.

The researcher must decide which sampling device and what size of sampler to use, and how many replicate samples to take for each population estimate. Comparisons of sampler accuracy are important to the interpretation of population statistics, but such comparisons are rarely made. The choice of sampler size is important because it may affect both the accuracy and precision of invertebrate population estimates. Small samplers are thought to yield overestimates of variables such as plant biomass due to edge effects (Hanson 1930; Sukhatme 1947; Hendricks 1956; Wiegert 1962; Van Dyne et al. 1963), while large samplers yield higher precision for the same level of replication (Smith 1938; Pechanec and Stewart 1940). Many ecologists have used large samplers to decrease sampling variability (Green 1979, p. 39), while other researchers have suggested that small samplers are the most cost effective (Smith 1938; Pechanec and Stewart 1940; Ursic and McClurkin 1959; Downing 1979; Green 1979, p. 38–39; John et al. 1980). Inaccurate sampler sizes should be avoided and the appropriate size of accurate sampling devices should be determined by the spatial variability of the organisms (Green 1979) and sampling costs (Cochran 1977, p. 84). The number of replicate samples (n) to be taken also depends upon the spatial distribution of the organisms and the desired level of precision of population estimates. In general, many replicate samples should be taken (Green 1979, p. 39) because the standard error (SE) of the mean is $\sqrt{s^2/n}$, where s^2 is the sampling variance. Provisional estimates of requisite sample number could be made if sampling variance could be predicted (Cochran 1977, p. 243; Elliott 1977, p. 129). To date, few comparisons of sampler accuracy have been made, and little is known about the spatial distribution of littoral invertebrates.

This article presents comparisons of the accuracy, precision, and efficiency of the Gerking, Macan, Minto, and KUG samplers with those of quadrat harvest techniques. We offer a preliminary analysis of spatial heterogeneity of littoral invertebrates as well as some recommendations on requisite sample number.

Methods

Accuracy

Two comparisons (A and B) of the relative accuracy of quadrat harvest (991 cm^2-square) and the Gerking, Macan, Minto, and KUG samplers were made during August of 1982. Some minor modifications were made over the original samplers (Fig. 1). Comparisons were made at 1 m depth in Lake Memphremagog, Quebec–Vermont (45°0′N, 72°17′W), near Cove Island (comparison A) and in Holbrook Bay (comparison B). In both cases, the macrophyte bed was composed of *Cabomba caroliniana*, *Elodea canadensis*, *Heteranthera dubia*, *Myriophyllum spicatum*, *Najas* sp., *Potamogeton gramineus*, *P. richardsonii*, and *Vallisneria americana*. The substrate was composed of sandy clay to clayey alluvium (A) and mud and clay (B). Median standing macrophyte biomass (dry weight) averaged 53 and 55 $g \cdot m^{-2}$, respectively.

In each comparison, the samples were taken at randomly drawn points along either side of a numbered 50-m line stretched at uniform depth across the macrophyte bed. Six replicate samples ($n = 6$) were taken with each sampler in each comparison. In quadrat samples, SCUBA divers clipped macrophytes, and plant and animal material was gently placed into 60 × 50 cm zippered 100-μm-mesh bags. Divers avoided edge effects by including every second plant found exactly on the edge of the quadrats. Samples were backwashed into a plastic bag using a jet of 100-μm-filtered lake water supplied by a self-priming pump. All other samplers were operated as described by Downing (1984) and all plant and animal material on inside surfaces was rinsed into the plastic bag. Samples were kept cold for transport to the laboratory.

In the laboratory, the organisms were rinsed from each piece of macrophyte with filtered lake water. The sample volume was reduced using a 21-cm-diameter filter funnel (Likens and Gilbert 1970) made with 100-μm nylon mesh. Samples were preserved in 80% ethanol. All organisms of major taxonomic groups in each sample were counted at 16× magnification.

Two comparisons (C and D) of the accuracy of different sizes of phytofauna samplers were made. Comparison C examined the sampling accuracy of five sizes of quadrat samplers: 112 ($n = 6$), 569 ($n = 4$), 991 ($n = 6$), 2540 ($n = 4$), and 10 002 cm^2 ($n = 3$). Comparison D examined in more detail the relative accuracy of the smallest (112 cm^2; $n = 10$) and medium-sized (991 cm^2; $n = 8$) quadrats. Samples in comparisons C and D were taken at different sites at 1 m depth in Cove Island Bay (Memphremagog), and quadrats were distributed randomly as before.

The significance of differences in sampling accuracy was determined using the Kruskal–Wallis test which tested the equivalence of distributions of population estimates obtained using different sampling methods (Conover 1980, p. 229). Comparisons of samplers were made for each of 20–30 taxonomic groups. Pairwise comparisons of sampling techniques were made using the Kruskal–Wallis multiple comparisons test (Conover 1980, p. 231).

Precision

Comparisons of the precision of samplers of different sizes were made by first finding the general relationship between sampling variance (s^2), size of mean observation ($\bar{x}$, i.e. population density of a taxon), and size of sampling unit (A; square centimetres) (Downing 1979). Second, analyses of departures from this general relationship were used to find whether some samplers yielded more variable observations than others (Downing 1984). Third, the general variance function was used to examine sample number requirements.

The replicate data derived in comparisons A–D and three other sets of observations taken from the same lake were used to derive a general variance function. The data collected consisted of arithmetic mean population estimates derived from sets of replicate samples of phytofauna taxa and taxonomic mixtures ($\bar{x}$; number per square metre), variances of these means (s^2), and sampler areas (A). The model

$$(1) \quad \log_{10} s^2 = a' + b \log_{10} \bar{x} + c \log_{10} A,$$

where a', b, and c are fitted constants, was fitted to the data by least squares regression. The residuals were plotted against the independent variables to ensure that no systematic lack of fit remained after analysis. Comparisons of the fit of subsets of the data (e.g. sampler type or taxon) were made using parametric methods (Prepas 1984).

Cost

The cost of different sampling strategies was considered in

order to optimize sampling programs (cf. Sheldon 1984). The three major costs in sampling the phytofauna are the time spent in (1) collection, (2) laboratory processing and preservation, and (3) counting of epiphytic invertebrate samples, assuming that equipment and data analysis costs are fixed with respect to sampling design. We measured the time spent on each stage of sampling using a waterproof chronograph. Cost estimates were then combined with predicted numbers of requisite samples to determine the most cost effective method of attaining a given precision.

Results and Discussion

Accuracy

Some aspects of sampler performance were obvious without quantitative analysis. Four samplers performed so poorly in comparisons A and B that many of the samples could not be used. Although every attempt was made to obtain phytofauna samples uncontaminated by sediments, 17% of the KUG samples, 25% of the Gerking and Minto samples, and 50% of the Macan samples had to be discarded due to contamination. Actual sample numbers for comparisons A and B thus were quadrat (6, 6), Gerking (6, 3), Macan (5, 1), Minto (5, 4), and KUG (6, 4), respectively. Unintentional collection of sediment was a more serious problem at the muddier site.

Three of the samplers were plagued with other difficulties. The Gerking sampler required that a diver reach through an opening and cut the macrophytes while sliding a door closed. It was impossible to do this without stirring the sediments. Macrophytes could not be cut uniformly at the sediment surface and some of the plants sank and were not collected. In addition, the structure was very heavy and cumbersome, required 50 L or more of filtered water for effective backwash, and water (and animals?) leaked out at the base between the door and the frame. The leaks could be alleviated by finer construction tolerances but the sampler would jam with mud, sand, shells, and plants. The Macan sampler was unwieldy and leaked for the same reason as the Gerking sampler. The Macan and Minto samplers uprooted plants more often than cut them. The KUG sampler was very cumbersome to use, requiring a stable boat and two operators. The blades dragged over plants before they were caught between the opposing blades, and plants were only rarely cut after they were caught. If the blades had been sharp enough to cut the macrophytes, the sampler would have been extremely dangerous to operate. The large net surface also required extensive backwashing.

Quantitative comparisons of population estimates agreed with field experience. Kruskal–Wallis tests of results obtained in comparisons A and B showed that there were significant ($P < 0.05$) differences in sampling accuracy of samplers in 46% of the taxonomic comparisons. In pairwise multiple comparisons (Fig. 2), samples collected using quadrat clipping by SCUBA yielded estimated population density distributions greater than or equal to those estimated by other techniques in 95% of taxonomic comparisons (Fig. 2). Quadrats yielded significantly greater ($P < 0.05$) population estimates in over 51% of taxonomic comparisons (Fig. 2). Where we found significant ($P < 0.05$) differences, population estimations made using quadrat clipping were an average of sevenfold greater than those made with other samplers (Table 1). Underestimates seem most severe for cladocerans and some types of gastropods. No differences could be detected for rare animals such as ephemeropterans, odonatans, and harpacticoid copepods. Highest population estimates were judged most accurate because all samplers are passive and there was little possibility of entraining organisms from outside the sampled area. Quadrat clipping yielded population estimates of some organisms more than 20-fold those found with other methods.

	QUADRAT	MINTO	MACAN	GERKING
MINTO	11 + 11 NS 3 −			
MACAN	12 + 12 NS 1 −	3 + 19 NS 3 −		
GERKING	13 + 12 NS 0 −	6 + 14 NS 5 −	7 + 13 NS 5 −	
KUG	15 + 9 NS 1 −	10 + 13 NS 2 −	4 + 21 NS 0 −	9 + 14 NS 2 −

FIG. 2. Accuracy comparisons A and B. Results of Kruskal–Wallis multiple comparisons tests (Conover 1980; p. 231) comparing the sampling accuracy of quadrat (991 cm^2) clipping with four other sampling devices for the estimation of phytofauna abundance. Comparisons are made for various taxonomic groups (e.g. Table 1). The values indicate the frequency with which the technique noted at the column head yielded significantly ($P < 0.05$) higher (+) or lower (−) population estimates than the technique noted at the left of the row. NS indicates the frequency with which no significant difference was found between sampling devices. Pairwise comparisons were made only where significant ($P < 0.05$) differences among techniques were indicated by Kruskal–Wallis one-way analysis of variance.

The KUG sampler was the poorest sampler, followed by the Gerking and Macan samplers. Differences were least pronounced between the Minto sampler and quadrat clipping (Fig. 2). Nematode population estimates were even higher using the Minto sampler than quadrat clipping (Table 1), which may reflect its sporadic inclusion of sediment in phytofauna samples.

The bite profiles of these samplers explain differences in sampling accuracy (Fig. 3). Only quadrat harvest by SCUBA cuts macrophytes directly at the sediment surface. The Gerking sampler requires that macrophytes be cut inside an enclosed space which cannot be uniformly at the sediment level. The Macan, Minto, and KUG samplers rely upon the opposition of a blade and cutting bar, and thus cannot remove all macrophyte and animal material from a sampled area.

Comparison C suggests that there were few significant differences among population estimates made using different quadrat sizes. Twenty comparisons of the sampling accuracy of different quadrat sizes were possible at the family to order level. Of these, none showed significant differences at the $P < 0.01$ level, and only estimates of oligochaete abundance and total organisms differed significantly among quadrat sizes at $P < 0.05$. According to a Kruskal–Wallis multiple comparisons test (Conover 1980, p. 231), the smallest quadrat size (112 cm^2) yielded highest estimates of these taxa ($P < 0.05$). Comparison D also showed few differences among the accuracy of different quadrat sizes. Out of 25 possible taxonomic comparisons, only two taxa were more accurately collected with a 112-cm^2 quadrat than a 991-cm^2 quadrat, while three taxa were less accurately collected

TABLE 1. Median number of organisms of various taxa per square metre estimated using quadrat clipping, and the ratios of these values with medians estimated using four other collection techniques. Ratios are computed only for those comparisons showing significant differences ($P < 0.05$) in Fig. 2; ns indicates no significant difference. A ratio >1 indicates that quadrat clipping yielded higher estimates for that taxon that the other technique.

	Comparison A					Comparison B			
		Ratio of medians					Ratio of medians		
Taxon	Median	Gerking	Macan	Minto	KUG	Median	Gerking	Minto	KUG
Acari	510	ns	5.2	ns	5.7	298	ns	ns	3.2
Chironomidae	4872	ns	3.3	2.3	8.8	1821	ns	ns	ns
Cladocera									
Camptocercus sp.	1564	10.4	ns	ns	ns	3026	ns	ns	ns
Chydorids	217	2.7	1.8	2.0	ns	243	7.4	3.1	ns
Cyclopoid copepods	439	2.5	ns	0.5	ns	1659	ns	ns	ns
Gastropoda									
Ancylidae	5	ns	ns	ns	ns	91	ns	ns	91.0[a]
Bulimidae	81	9.5	ns	3.1	4.3	35	ns	ns	ns
Physidae	91	ns	7.6	8.6[a]	5.5	1059	ns	ns	19.6
Planorbidae	4499	4.3	ns	5.7	ns	308	ns	ns	ns
Species "L"	691	2.3	3.5	13.0	20.6	1650	ns	ns	3.0
Other gastropods	10	ns	ns	ns	ns	40	ns	ns	5.7
Lepidoptera	86	3.4	ns	un[b]	5.7	20	ns	ns	ns
Nematoda	136	ns	ns	ns	ns	7[a]	ns	0.0	ns
Pelecypoda	40	ns	ns	ns	ns	0	0.0	0.0	0.0
Turbellaria	5	un[b]	ns	un[b]	ns	5	ns	ns	ns
Trichoptera	56	2.0	4.6	ns	13.9	25	ns	un[b]	ns
Total organisms	17365	2.3	ns	ns	4.0	16437	2.6	ns	2.0

[a]Mean used in denominator to avoid undefined ratio.
[b]Both median and mean of denominator is zero. Ratio undefined.

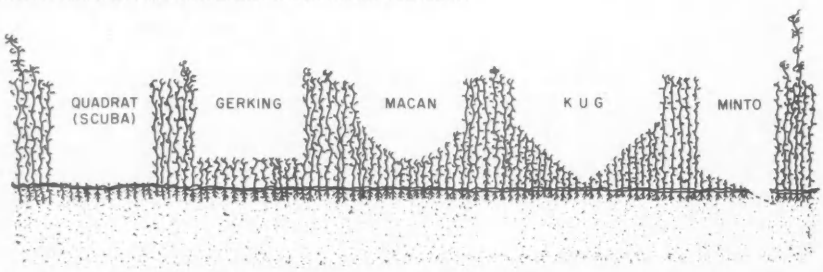

FIG. 3. Schematic bite profiles of phytofauna samplers showing the amount of macrophyte removed by various samplers.

(Table 2). We conclude, therefore, that differences in collection accuracy of different sizes of quadrats are small.

Precision

We found a high degree of variation among replicate population estimates of the epifauna. Regression analysis (equation 1) showed that much of the variation in $\log_{10} s^2$ of replicate samples could be accounted for by mean population density and sampler size (Table 3). The data consist of 497 separate observations and are not published here.[2] The range of estimated mean population density was from 0.3 to 27 600 organisms·m^{-2}, the variance from 0 to 1.8×10^8, sampler area from 111.8 to 10 002 cm^2, and number of replicate samples from 3 to 20. When considered on a square metre basis, epiphytic invertebrates appear highly aggregated because $s^2 > \bar{x}$ in more than 99% of the observations collected. The regression equation ($R^2 = 0.94$; $n = 497$) characterizing the sampling variance of taxa and taxonomic mixtures is

$$(2) \quad \log_{10} s^2 = 1.831 + 1.640(\log_{10} \bar{x}) - 0.435(\log_{10} A)$$

or

$$(3) \quad s^2 = 67.76\bar{x}^{1.640}A^{-0.435}$$

[2]A complete set of tabular data is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2.

TABLE 2. Comparison D of the population estimates of various taxa obtained clipping a small (112 cm^2; $n = 10$) and medium (961 cm^2; $n = 8$) sized quadrat. Values in columns 1 and 2 are estimated median population density (no. $\cdot m^{-2}$). Comparisons were made using the Mann–Whitney test (Conover 1980, p. 216). P is the computed probability that the distributions of estimates drawn using the two quadrat sizes are equivalent: $*P < 0.05$; $**P < 0.01$.

Taxon	Estimated median density		Mann–Whitney test	
	112 cm^2	991 cm^2	U	P
Acari	894	1 144	30	0.41
Amphipoda	0	15	37	0.83
Chironomidae	4 472	3 999	39	0.97
Cladocera				
Alona sp.	0	40	31	0.46
Camptocercus sp.	1 655	756	19	0.07
Chydorids	268	181	35	0.70
Sida crystallina	223	55	26	0.20
Cyclopoid copepods	4 248	842	6	<0.01**
Gastropoda				
Ancylidae	0	25	27	0.24
Bulimidae	89	40	21	0.10
Miscellaneous	0	25	24	0.17
Physidae	45	150	34	0.63
Planorbidae	223	454	16	0.03*
Species "L"	268	126	28	0.31
Hirudinea	0	20	10	0.01**
Lepidoptera	44	20	38	0.83
Nematoda	626	555	39	0.97
Oligochaeta	2 562	1 200	26	0.24
Ostracoda	5 769	2 976	13	0.02*
Turbellaria	805	514	36	0.76
Trichoptera	0	35	15	0.03*
Total organisms	29 785	15 201	23	0.15

TABLE 3. Analysis of variance table for regression of $\log_{10} s^2$ as a function of $\log_{10} \bar{x}$ (average phytofauna density; no. $\cdot m^{-2}$) and $\log_{10} A$ (sampler area; cm^2) (equations 1 and 2). F' (partial F-value) is calculated as the increase in model SS when the independent variable is entered into the multiple regression as the last variable. F' is a measure of the variation in $\log_{10} s^2$ accounted for by each independent variable. The probability of obtaining any of these F or F' values by chance is $\ll 0.001$.

	df	SS	F	R^2	F'
Source of variation					
Model (equation 1)	2	1272	3825	0.94	
Error	494	82			
Total	496	1354			
Independent variable					
$\log_{10} \bar{x}$					6401
$\log_{10} A$					131

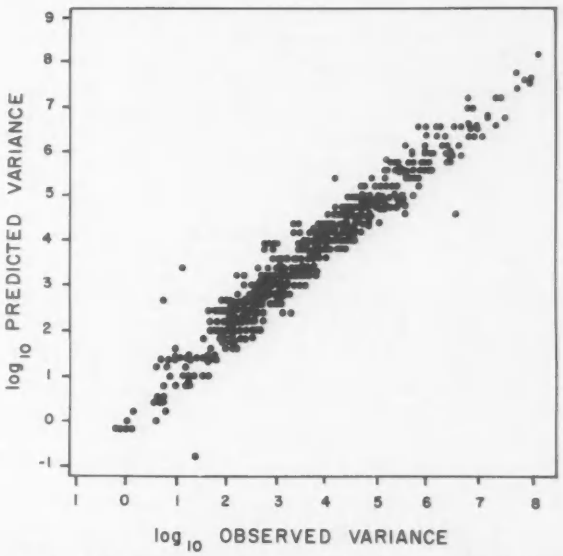

FIG. 4. Relationship of variances predicted from equation 2 to observed variances for epiphytic invertebrate taxa keyed to taxonomic levels indicated in Table 5. The data are clustered around a 1:1 correspondence, indicating good fit of equation 2 to the observed patterns of spatial variability.

where all variables are as in equation 1. In general, the function fits the data very well, and predicted variances show a 1:1 correspondence with observed variances (Fig. 4). Other regression models were attempted, including models containing interaction terms, but this one proved to be the most accurate and precise. Table 4 shows that no sampling technique yielded residuals that differed significantly ($P < 0.05$) from the overall variance function. Thus, equation 3 appears to work equally well regardless of sampling device.

The small residual variability in equation 2 (approximately 6% of total; Table 3) indicates that most of our phytofaunal taxa were aggregated to a similar degree. Table 5 shows the residuals from equation 2 averaged over a variety of taxonomic groups. Analysis of the residuals indicates the relative degree to which epiphytic invertebrate taxa were aggregated. A positive average residual for a taxonomic group would suggest that observed variances for the group are larger than the average residual of the entire dataset (i.e. 0). Larger residuals thus infer a greater degree of spatial aggregation (Taylor 1961, 1980; Downing 1979, 1980, 1981). The t-values in Table 5 indicate that few taxonomic groups have residuals that differ significantly ($P <$ 0.05) from the overall mean. This appears to be true at all levels of taxonomic detail. These analyses show that beetles, caddisflies, and water mites are less aggregated than average, while only a single type of ostracod is more aggregated than average. This shows that the intercepts (a'; equation 1) are nearly homogeneous among taxa.

A test for intertaxonomic differences in slope (b) of the variance relationship (equation 1) is provided in the last column of Table 5. Shown are coefficients of determination (r^2) for the correlation between the residuals from equation 2 (in $\log_{10}$ form) and the logarithm of mean population density ($\log_{10} \bar{x}$). The table shows that there are four significant correlations but only one (Coleoptera) accounts for >50% of the variation in the residuals. All taxa do not fit perfectly, but at least for lumped taxa such as those analyzed here, equation 3 should give general

TABLE 4. Analysis of residuals (in $\log_{10}$ form) from equation 2 by type of sampler. A mean residual of 1.0 would indicate that sampling variances are, on average, 10 times the predicted values and a mean residual of −1.0 indicates that sampling variances average 1/10 the predicted values. n is the number of sets of samples collected using each sampling device, and t is the t-statistic comparing the mean residual of the subgroup (i.e. sampler) with the average of the residuals of all other subgroups assuming unequal variances (Prepas 1984). No sampler yielded variances that departed significantly ($P < 0.05$) from the pattern described by equation 2.

Sampling device	n	Mean	Variance	t	df
Quadrat (569 cm^2)	26	0.092	0.092	1.56	30
KUG Sampler	54	0.056	0.244	0.90	62
Quadrat (991 cm^2)	198	0.037	0.114	1.76	486
Quadrat (112 cm^2)	47	0.007	0.095	0.15	65
Gerking Sampler	50	0.007	0.154	0.12	62
Quadrat (2540 cm^2)	24	−0.080	0.110	−1.20	27
Minto Sampler	48	−0.096	0.266	−1.38	53
Macan Sampler	26	−0.111	0.168	−1.42	16
Quadrat (10,002 cm^2)	24	−0.167	0.487	−1.22	24

guidance regarding the degree of spatial heterogeneity to be encountered in the field. Equation 3 works equally well (t-value = −1.42; df = 136; P of difference is 0.16) for both of the study sites examined. Individual species or other sites could depart radically, however, and pilot field studies should be used if time and research funding permit.

Assuming that the epifauna in Lake Memphremagog are representative, equation 3 can be used to calculate provisional estimates of the number of replicate samples ($\hat{n}$) that one must take to yield a given level of precision. The predicted variance can be calculated by rearranging equation 1:

$$(4) \quad s^2 = a\bar{x}^b A^c$$

(analogous to equation 3) where $a = 10^{a'}$ and all other variables are as in equation 1. The predicted number of samples ($\hat{n}$) needed to obtain a given level of precision can be calculated by

$$(5) \quad \hat{n} = a\bar{x}^{b-2}A^c p^{-2}$$

where p is the desired ratio of the standard error (SE) to the mean population density ($\bar{x}$). If we desire a level of precision that is equal to, say, 20% of the mean (a value suggested by Elliott 1977, p. 129), then $p = 0.2$ and $\text{SE} = 0.2\bar{x}$.

For the freshwater epiphytic invertebrate fauna in Lake Memphremagog, the regression coefficients can be substituted into equation 5 to yield

$$(6) \quad \hat{n} = 67.76\bar{x}^{-0.360}A^{-0.435}p^{-2}.$$

This equation shows that the requisite number of replicate samples increases with decreased population density, decreased sampler area, and increased precision (i.e. decreased p). If equation 6 holds for other ecosystems, predictions of $\hat{n}$ could be made by guessing the population levels to be encountered in the field, or through the use of preliminary sampling surveys.

TABLE 5. Analysis of residuals from equation 2 by taxonomic group. All variables are as in Table 4. r^2 is the coefficient of determination for the relationship between the residuals in $\log_{10}$ form and $\log_{10}\bar{x}$ for each taxon. The prefix "total" indicates that members of the taxonomic group were summed within each sample before means and variances were calculated among replicates. *$P < 0.05$; **$P < 0.01$.

Taxon	Organisms keyed to:	n	Mean	Variance	t	df	r^2
Ostracod type "S"	Genus(?)	15	0.194	0.107	2.37*	15	0.00
Odonata	Order	8	0.171	0.076	1.75	8	0.07
Tardigrada	Class	3	0.147	0.047	1.17	2	0.30
Total Ostracoda	Order	21	0.145	0.397	1.94	22	0.06
Ephemeroptera	Order	9	0.128	0.110	1.17	8	0.02
Pelecypoda	Class	15	0.119	0.397	0.75	14	0.37*
Harpacticoid copepods	Suborder	15	0.114	0.116	1.30	15	0.02
Nematoda	Order	19	0.109	0.103	1.50	20	0.01
Chironomidae	Family	21	0.103	0.360	0.81	21	0.03
Oligochaete type "L"	Genus(?)	9	0.098	0.104	0.92	8	0.13
Total organisms	Kingdom	21	0.094	0.198	0.99	21	0.10
Turbellaria	Class	10	0.082	0.054	1.09	10	0.37
Total Gastropoda	Class	5	0.060	0.082	0.46	4	0.24
Hirudinea	Class	14	0.059	0.093	0.73	14	0.39*
Ceratopogonidae	Family	4	0.054	0.154	0.28	3	0.38
Hydra sp.	Genus	21	0.025	0.169	0.28	22	0.03
Total Oligochaeta	Order	21	0.006	0.227	0.06	21	0.02
Gammarus sp.	Genus	21	−0.006	0.080	−0.10	24	0.02
Misc. Gastropoda	Family[a]	108	−0.033	0.108	−1.09	217	0.00
Cladocera	Genus[b]	57	−0.063	0.225	−1.09	67	0.06
Lepidoptera	Order	12	−0.103	0.122	−1.03	12	0.05
Cyclopoid copepods	Suborder	20	−0.115	0.065	−1.99	23	0.07
Coleoptera	Order	8	−0.173	0.008	−4.80**	13	0.57*
Trichoptera	Order	18	−0.207	0.077	−3.17**	20	0.07
Acari	Order	21	−0.321	0.442	−2.29*	21	0.02

[a]ANCOVA shows that there is no significant ($P < 0.01$) heterogeneity of a' or b (equation 1) among families within this class.

[b]ANCOVA shows that there is no significant ($P < 0.01$) heterogeneity in a' or b (equation 1) among genera within this order.

TABLE 6. Number of replicate samples needed for various sampler sizes and phytofauna population densities in order that the SE of replicate samples averages 20% of the mean population density ($p = 0.2$). Calculations are from equation 6.

Population density (no.·m^{-2})	Area covered by sampling device (cm^2)				
	112	569	991	2540	10 002
1	218	107	84	56	31
10	95	47	37	24	13
100	41	20	16	11	6
1 000	18	9	7	5	3
10 000	8	4	3	2	2

Table 6 shows the approximate number of phytofauna samples needed at different levels of population density using different sized sampling devices. These predictions are made for average phytofaunal taxa.

Cost Efficiency

Table 6 shows that equally precise population estimates of epiphytic invertebrates can be made using a variety of combinations of sampler size (A) and sample number (n). Decisions as to what combination to use must be based on cost considerations. Our measurements show that between 52 and 78% of the costs are due to counting of samples (Table 7). Collection takes the least time (4–8% of total), while processing samples takes a little more (7–31% of total). Table 7 shows that per-sample costs at all stages of analysis rise rapidly with the size of sampling device. We used regression analysis to test for the multiple effects of size of sampling device, standing macrophyte biomass, and total population density of littoral invertebrates on the total time necessary to extract, process, and count a sample of the epifauna (Table 8). We found that the total sampling cost (T; minutes) was only a significant function ($P < 0.05$) of the size of sampling device (A; square centimetres) and the standing macrophyte biomass (B; grams dry weight per square metre):

$$(7) \quad T = 5.18 + 0.032A + 1.190B.$$

TABLE 7. Average amount of time-cost (min) for each phytofauna sample during each stage of sample collection. Data were collected during comparison C (average macrophyte biomass: 19 g dry wt.·m^{-2}). Values in parentheses are the number of samples and the standard deviation of time measurements.

Quadrat area (cm^2)	Sampling cost (min·sample^{-1})			
	Collection	Processing	Counting	Total
112	1.8 (6, 0.6)	6.5 (5, 1.6)	12.3 (6, 7.8)	21.0 (5, 8.3)
569	3.3 (4, 1.2)	7.7 (4, 3.3)	22.7 (4, 16.4)	33.7 (4, 20.5)
991	4.8 (6, 1.4)	10.6 (6, 3.1)	30.5 (5, 13.5)	44.5 (5, 15.0)
2 540	5.3 (4, 0.8)	11.1 (4, 2.5)	58.0 (4, 25.3)	74.3 (4, 28.3)
10 002	14.6 (3, 2.7)	24.5 (3, 5.8)	184.5 (3, 166.5)	356.9 (3, 157.0)

TABLE 8. Analysis of variance table for regression of total time required to collect, process, and count phytofauna samples (T; min) as a function of the area covered by the sampling device (A; cm^2) and the standing biomass of aquatic macrophytes (B; g dry wt.·m^{-2}) (equation 7). All variables are as in Table 3.

	df	SS	F	R^2	F'
Source of variation					
Model (equation 8)	2	466,995	57	0.50	
Error	114	472,025			
Total	117	939,020			
Independent variable					
A					110
B					8

Invertebrate population density had no significant effect on sampling cost. This suggests that it is the searching through detritus and plant material for animals that took the most time, not the actual counting and identification of the animals. This might not be true had taxonomic identification been more detailed.

We have used actual average cost estimates made under one set of conditions (Table 7) to examine the cost efficiency of different sampler sizes. Average total time-costs from Table 7 can be substituted into Table 6 to yield predicted average sampling costs for various sampling regimens. These results (Table 9) show that sampling costs are highest when sparse populations are estimated using large area samplers. The optimal sampler size for the phytofauna seems to be between 100 and 1000 cm^2. Quadrats of 500 cm^2 are in this range and would yield convenient calculations. The total cost per unit area for 112-cm^2 samplers is 0.19 min·cm^{-2} as compared with 0.06 min·cm^{-2} for 569-cm^2 samplers. Smallest samplers are somewhat more costly because very small samplers require about the same amount of time to approach and retrieve as larger ones.

Labour savings due to sampler choice can be quite substantial. The most common sampler size used for the phytofauna has been 2500 cm^2 (e.g. Calow 1973; Andrikovics 1975; McLachlan 1975; Soszka 1975; Chambers 1977; Junk 1977). The substitution of a 569-cm^2 sampler could result in time savings of between 9 and 18% (Table 9), depending upon the density of the target population. Substitution of a 569-cm^2 quadrat for a 1-m^2 sampler could result in a threefold to fivefold

TABLE 9. Average amount of time (min) needed to collect, process, and count sufficient phytofauna samples such that the SE of replicate samples averages 20% of the mean estimated population density ($p = 0.2$). Calculations were made by multiplying the predicted sample numbers ($\hat{n}$) in Table 6 by the average total collection times indicated in the last column of Table 7. Actual values will differ under other conditions (see equation 7). The table shows that, in general, larger samplers result in more expensive sampling programs.

Population density (no.·m^{-2})	Area covered by sampling device (cm^2)				
	112	569	991	2540	10 002
1	4571	3606	3741	4161	11 064
10	1992	1584	1648	1783	4 640
100	860	674	712	817	2 141
1 000	377	303	312	372	1 071
10 000	168	135	134	149	714

reduction in sampling effort. In addition to their greater efficiency, small samplers yield samples that are easier to store and transport, and destroy between one-fifth and one-ninth the amount of habitat for the same level of precision. This is especially important for studies involving seasonal dynamics of invertebrates in small weed beds.

Recommendations

Our comparisons of sampler accuracy indicate that quadrat clipping techniques yield the highest population estimates. These population estimates are commonly fivefold greater than those made using the Gerking, Macan, Minto, or KUG samplers (Table 1). All five quadrat sizes tested appear to yield similar population estimates. The most accurate method is therefore the gentle removal of macrophytes from quadrat frames.

The number of requisite replicate samples depends upon the size of the quadrat used and the population density of the organism of interest. The number of replicate samples taken must be large if sparse populations are being studied, small samplers are being used, or high levels of precision are required. Our estimates of sampling variance made in Lake Memphremagog could be used to make preliminary estimates in other ecosystems. The provisional sample number can be predicted from equation 6. Our examination of sampling costs shows that the amount of time expended per phytofauna sample increases rapidly with sampler size and macrophyte standing biomass (Table 8). Combination of these data with predicted sample number shows that optimal quadrat sizes were between 112 and 991 cm^2. We therefore recommend that phytofauna population estimates be made by counting the organisms collected through the gentle clipping of macrophytes within 500-cm^2 quadrats. These population estimates should be among the most accurate, precise, and cost effective possible using current technology. It should be remembered that even at moderate macrophyte biomass, the processing of a single set of samples with sufficient replication to describe population densities of 1 organism$\cdot m^{-2}$ with a precision ($SE/\bar{x}$) of 0.2 has an average cost of over 60 h. Even optimally designed sampling programs are costly. The littoral ecologist must therefore choose hypotheses carefully.

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Genetic Variation in Atlantic Cod (*Gadus morhua*) Throughout Its Range

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The amount of genetic differentiation between stocks of Atlantic cod (*Gadus morhua*) was estimated from electrophoretically detectable protein loci expressed in skeletal muscle and liver. Variant alleles at 13 of these loci were detected among nine samples covering most of the species range: North America, Greenland, Iceland, Barents Sea, Norwegian coastal waters, the North Sea, and the Baltic Sea. A very low amount of genetic differentiation was observed among stocks. Only two loci (*LDH-3* and *PGI-1*) showed large statistically significant heterogeneity of allele frequencies between samples. Standard genetic distances (Nei) between these samples based on 10 variable loci ranged from 0.00015 to 0.01072 with Baltic cod as the genetically most divergent sample. There was a highly significant correlation between genetic and geographic distance for the samples from the Atlantic suggesting that a substantial gene flow has occurred between these stocks with geographic distance being an inhibiting factor. The relatively larger genetic distance between the Baltic cod and other stocks may reflect isolation resulting from geographic and perhaps ecological barriers. However, the absolute amount of genetic differentiation in the Atlantic cod appears to be very low throughout its range.

Les auteurs ont déterminé le niveau de différenciation génétique entre des stocks de morue franche (*Gadus morhua*) à l'aide de loci protéiques révélés par électrophorèse dans les muscles squelettiques et la foie. Des allèles variants ont été découverts à 13 de ces loci dans neuf échantillons provenant de presque toute l'aire de répartition de l'espèce : Amérique du Nord, Groenland, Islande, mer de Barents, eaux côtières de la Norvège, mer du Nord et mer Baltique. Les auteurs ont observé un très faible niveau de différenciation génétique entre les stocks. Seuls deux loci (*LDH-3* et *PGI-1*) ont démontré une forte hétérogénéité statistiquement significative des fréquences alléliques d'un échantillon à l'autre. Les distances génétiques normalisées (Nei) entre ces échantillons, établies à partir de 10 loci variables, ont varié de 0,00015 à 0,01072; la morue de la mer Baltique représentait l'échantillon le plus différent au point de vue génétique. Il existait une corrélation fortement significative entre les distances génétique et géographique chez les échantillons recueillis dans l'Atlantique, ce qui porte à croire qu'un important échange de gènes a eu lieu entre ces stocks, quoique la distance géographique ait agi comme facteur inhibiteur. La distance génétique relativement plus élevée entre la morue de la mer Baltique et les autres stocks peut traduire une isolation causée par des obstacles géographiques et peut-être écologiques. Toutefois, le niveau absolu de différenciation génétique de la morue franche semble très faible dans toute son aire de répartition.

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The reproductive relationships and the amount of genetic divergence between the various stocks of Atlantic cod (*Gadus morhua*) are currently under debate. On one hand, tagging experiments have revealed interstock exchanges of specimens potentially reflecting a considerable amount of gene flow (Hansen 1949; Jensen 1953; Joensen 1953; Rollefsen 1953; Rasmussen 1959; Gulland and Williamson 1962; Tiews and Lamp 1974; Templeman 1974, 1976, 1979; Godø 1983). This concept of a considerable amount of gene flow is supported by some genetic studies based on electrophoretic data indicating little genetic differentiation throughout large parts of the species range (Odense et al. 1969; Lush 1970;

Mork et al. 1980; Mork and Sundnes 1983). On the other hand, investigations that also used electrophoretic and, in some instances, immunochemical characteristics (blood groups) suggested the existence of genetically discrete subpopulations, sometimes within very restricted geographic areas (Frydenberg et al. 1965; Sick 1965a, 1965b; Møller 1967, 1968, 1969; Jamieson 1975; Cross and Payne 1978).

There are no reports on quantification of the actual amount of genetic divergence between stocks of Atlantic cod. The traditional classification of cod into races and subspecies (Schmidt 1930; Svetovidov 1948) is based on meristic traits, and there is no information on the genetic basis for the variation of these characters. Hence there is a strong need for genetic data which may delineate the genetic relationships and estimate the amount of divergence between stocks of cod. Such information is most conveniently obtained through the study of a large number of electrophoretically detectable protein loci. Our objective was to analyze the genetic variability pattern at 19 electrophoretic loci in Atlantic cod sampled from nine locations distributed over most of the species' range.

Materials and Methods

Pertinent data for the nine locations are given in Table 1 and Fig. 1. Tissue samples were stored for up to 2 yr at −20 to −75°C before electrophoretic analysis. Extracts of white skeletal muscle and liver from each specimen were analyzed by starch gel electrophoresis, as described in Mork et al. (1982). Three buffer systems were used:

(I) (Ridgway et al. 1970) — gel: 0.03 mol/L Tris – 0.006 mol/L citric acid, pH 8.5; electrode: 0.06 mol/L lithium hydroxide – 0.3 mol/L boric acid, pH 8.1.

(II) (Clayton and Tretiak 1972) — gel: 0.002 mol/L citric acid, pH 6.0; electrode: 0.04 mol/L citric acid, pH 6.1; both buffers were pH adjusted with *N*-(3-amino-propyl)-morpholine.

(III) (Markert and Faulhaber 1965) — gel: 1:4 dilution of electrode solution; electrode: 0.18 mol/L Tris – 0.1 mol/L boric acid – 0.004 mol/L EDTA.

The methods used for visualizing 12 enzymes and one unidentified protein are described by Allendorf et al. (1977) and Harris and Hopkinson (1976). These proteins were (abbreviation and Enzyme Commission No. in parentheses) aspartate aminotransferase (AAT; 2.6.1.1), creatine kinase (CK; 2.7.3.2), glyceraldehydephosphate dehydrogenase (GAP; 1.2.1.12), glycerol-3-phosphate dehydrogenase (G3P; 1.1.1.8, previously noted as alpha-glycerophosphate dehydrogenase (α-GPDH) by Mork et al. 1982), isocitrate dehydrogenase (IDH; 1.1.1.42), lactate dehydrogenase (LDH; 1.1.1.27), malate dehydrogenase (MDH; 1.1.1.37), phosphoglucoisomerase (PGI; 5.3.1.9), phosphoglucomutase (PGM; 2.7.5.1), reducing enzyme (RE), sorbitol dehydrogenase (SDH; 1.1.1.14), and superoxide dismutase (SOD; 1.15.1.1). The CK bands obtained by specific staining corresponded perfectly to a set of sharply defined bands visualized by general protein staining (Coomassie Brilliant Blue R-250) which was subsequently used for CK typing. This allowed the simultaneous scoring of a yet unidentified muscle protein (MP) anodal to and well separated from the CK bands. MP is expressed as an electrophoretically monomeric protein; variants appear as equally intense staining double bands. The bands attributed to RE occurred as unstained zones against a bluish background on gels where staining recipes included phenazine methosulphate (PMS) and the tetrazolium dye MTT (S. Grant, Department of Microbiology, University of Cape Town, Rondebousch 7700, South Africa, pers. comm.).

Our genetic interpretation of electrophoretic banding patterns follows Allendorf et al. (1977), and the system of nomenclature is that of Allendorf and Utter (1979). Information on the electrophoretic expression of CK, GAP, G3P, and RE was kindly provided by S. Grant (pers. comm.). The *PGM-1* locus in the present report corresponds to *PGM* in Mork et al. (1982); otherwise the present nomenclature is concordant with that report.

TABLE 1. Atlantic cod sampling information. Map codes refer to Fig. 1.

Map code	Stock and sample location	Date of sampling	Number of fish	Gear	Age range (yr)	Sex ratio (% females)
A	North America (Gulf of Maine)	Nov. 1982	97	Trawl	0–8	66
B	Greenland (Dana Bank)	Dec. 1982	96	Trawl	3–6	57
C	Iceland (Faxafloi)	Mar. 1983	100	Gill Net	4–10	56
D	Arcto-Norwegian (Barents Sea)	Aug. 1982	96	Trawl	0-group	
E	Norwegian coastal (Malangen)	Sept. 1982	96	Trawl	0-group	
F	Norwegian coastal (Trondheimsfj.)	Apr. 1981	96	Trawl	3–9	3
G	Norwegian coastal (Oslofjorden)	Dec. 1981	100	Trap net	1–3	59
H	North Sea (Lowestoft)	Nov. 1981	100	Trawl	1–6	59
I	Baltic Sea (Gotland)	Jan. 1982	99	Gill Net	3–6	66

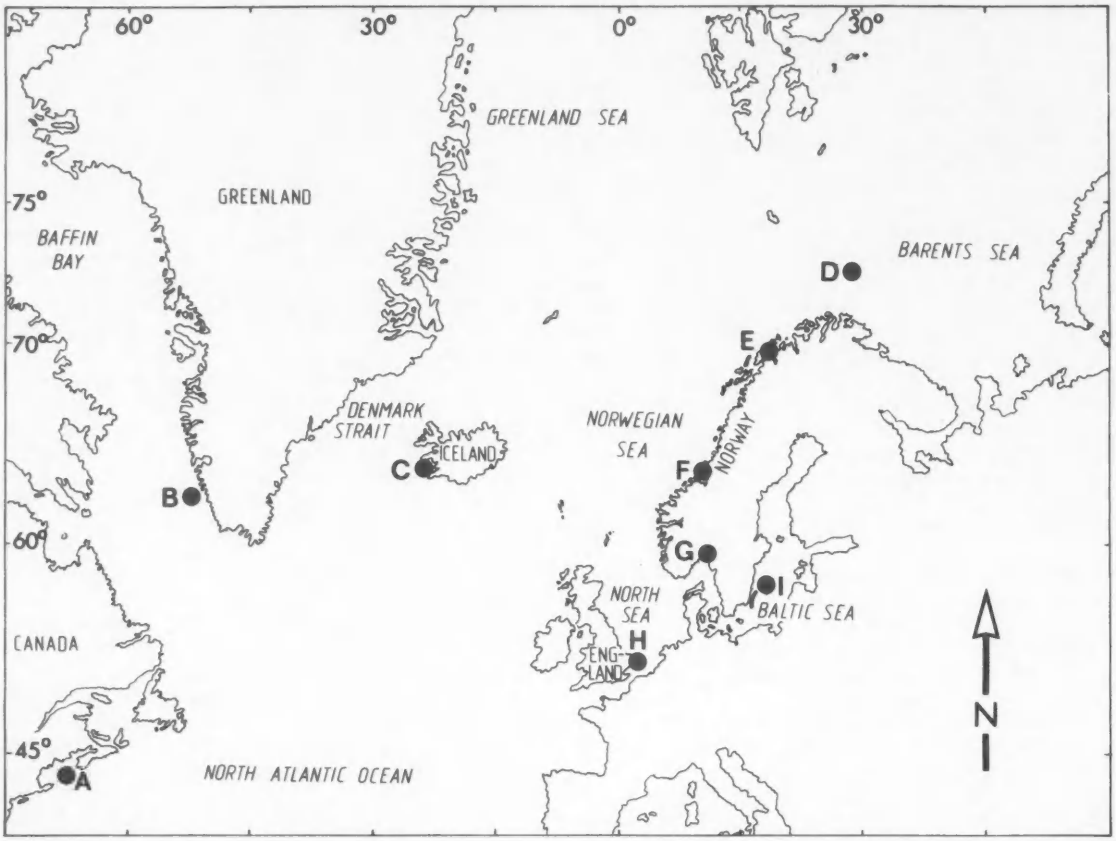

FIG. 1. Geographic location of Atlantic cod sampling areas (cf. Table 1) (high-latitude land masses are correct in relative position, although their sizes are exaggerated).

The prime purpose of our present study was to analyze the genetic population structure and not to estimate electrophoretic heterozygosity from randomly selected loci (see Mork et al. (1982) and Grant (in press) for such estimates). The tissue samples were collected over an extended period of time and stored under different conditions before the electrophoretic analysis. As a consequence, enzyme activity varied considerably among samples, and it was not possible to score reliably all the 19 loci in all samples. Because of our major purpose to delineate population structure, we chose to concentrate on loci that had been variable in previous studies (Mork et al. 1982; Grant, in press) when analyzing samples with reduced enzymatic activity.

When performing statistical tests the deviation between the observed distribution and that expected under the null hypothesis was considered significant at $P < 0.05$; all tests were treated as independent ones, and no corrections were made to account for possible effects due to multiple testing. Exact probabilities of observed genotypic distributions under the assumption of Hardy–Weinberg equilibrium were computed using an extended version of the test described by Vithayasai (1973). The *G*-statistic (Sokal and Rohlf 1981) was used for contingency tests of allele frequency homogeneity. Variant alleles were pooled in order to obtain, as far as possible, sufficiently high expected values in the *G*-tests. Standard genetic distance values were calculated according to Nei (1972). A dendrogram was constructed using the unweighted pair-group method (UPGM, Sneath and Sokal 1973) based on the genetic distance matrix of those values. A gene diversity analysis (Nei 1973a; Chakraborty et al. 1982) was used for partitioning the total gene diversity into its components within and between samples. Geographic distances were measured as the shortest marine route between the locations sampled.

The specimens were sexed in all samples except D (Malangen) and E (Barents Sea). Age determination was performed by otolith reading according to Rollefsen (1933).

Results and Discussion

Description of Loci and Allelic Variants

A total of 19 loci were detected from the 13 protein systems, and variant alleles were observed at 13 of these loci (Table 2). Although several of the loci have been described earlier (Mork et al. 1982; Grant, in press), a number of previously undescribed alleles were found to segregate in our present material (Table 2).

The number of loci yielding reliable data varied among locations (Table 3). Insufficient enzyme activity due to storage effects did not permit reliable scoring of more than 10 loci for four of the locations (B, D, E, and I). Two average heterozygos-

TABLE 2. The 19 loci scored in Atlantic cod including the combinations of tissue and buffer showing the best resolution, and designation of variant alleles (see text for description of buffer systems and locus abbreviations). L = liver, M = muscle.

Locus	Buffer system	Best tissue (ranked)	Variant alleles
AAT-1	II	L, M	
-2	II	L	*-50*[a]
-3	II	L	
CK-1	I	M	*85*[a], *105*[a]
GAP-1	II	M	
G3P-1	II	M	*-300*[a], *-100*[a], *200*[a]
IDH-1	II	L	*140*
-2	II	M, L	*50*[a], *200*[a]
LDH-1	II	L	
-2	II	M, L	*95*[a]
-3	II	L, M	*70*, *85*[a], *140*[a]
MDH-3	II	L, M	*60*
MP	I	M	*90*
PGI-1	I	M, L	*65*, *97*[a], *135*, *160*[a]
-2	I	L, M	*90*
PGM-1	I	M, L	*70*, *80*, *120*[a]
RE	III	M	
SDH-1	I	L	*-100*[a]
SOD	I	M	

[a]Allele not previously reported.

ity values are therefore given; one is based on the 10 loci scored in all samples, and another is based on the 19 loci scored in samples A, C, F, G, and H. The highest levels of genetic variability are found at *LDH-3* and *PGI-1* (Table 3). A recent study by Mork and Sundnes (1985b) indicated that these two loci may be affected by selection. Those authors observed differential survival of genotypes when attempting to artificially feed cod fry that were caught in the sea and brought to an aquarium. It cannot be evaluated whether or not selection has affected the genotypic distributions of the natural populations sampled in our present study. However, the results reported by Mork and Sundnes (1985b) should be kept in mind when interpreting the current data.

Within-Sample Variation

Tests for deviations from Hardy–Weinberg expectations and for the homogeneity of allele frequencies between sexes were applied to all variable loci in all samples. The only statistically significant deviation from Hardy–Weinberg expectations occurred in sample D (Barents Sea; excess of heterozygotes at *PGI-1* with $P = 0.028$). Three of four observed statistically significant allele frequency differences between sexes occurred in sample G (Oslofjorden: *G3P-1*, $P = 0.023$; *MDH-3*, $P = 0.018$; and *PGI-1*, $P = 0.009$); the fourth deviation occurred in sample A (Gulf of Maine: *LDH-3*, $P = 0.022$).

There was an excess of females in all sexed samples except F which consisted almost entirely of males. Skewed sex ratios are not infrequently observed in catches of adult cod and may result from sexual differences in size (growth), maturing age, mortality, or behavior. However, the literature on this subject is scarce (O. R. Godø, Institute of Marine Research, P.O. Box 1870, N-5011 Nordnes, Norway, pers. comm.).

The present data provide no explanation for the disproportionate distribution of alleles between sexes in sample G. Testing all pairwise combinations of variable loci within this sample for gametic phase disequilibrium (Hill 1974) yielded no significant deviations from random association. Further sampling is required to determine whether the allele frequency differences observed reflect selection, as yet unidentified population subdivision, or mere coincidence. At any rate, this disproportionality between sexes within sample G had to be disregarded in the subsequent analyses, and it appears to be of little relevance for our conclusions regarding the genetic differentiation pattern over large geographic distances.

The two values of average heterozygosity ($\bar{H}$) provide somewhat different information. The values based on 19 loci available for five of the samples provide an overall estimate yielding a restricted range of 0.068–0.079 with a mean of 0.071. The heterozygosity values from the 10 variable loci reflect the relative variability within all the samples, with extreme values found at the adjacent Oslofjorden (0.145) and Baltic Sea (0.112) locations.

Between-Sample Variation

Allele frequencies at variable loci were tested for between-sample homogeneity after pooling of variant alleles (Table 3). The overall heterogeneity was highly significant as evaluated from the sum of G-values from all contributing loci (sum of $G = 189.5$, df = 96, $P \ll 0.001$). Highly significant heterogeneity occurred at the *LDH-3* locus, which distinguished sample I (Baltic Sea) from the remaining samples, and at the *PGI-1* locus, where the two most western samples (A, Gulf of Maine; B, Greenland) stand out from the remainder. The sum of G-values from all loci is no longer statistically significant if the contributions from *LDH-3* and *PGI-1* are excluded from the analysis ($G = 95.6$, df = 80, $P > 0.10$). The gene diversity analysis reflected an overall low level of genetic differentiation with only 2.1% of the total diversity distributed between samples. Approximately half of this variation among samples is due to differences between the Baltic Sea and the other samples (1.0% out of the 2.1%).

The observation of a low amount of genetic heterogeneity with conspicuous allele frequency differences found at two loci only is clearly reflected by the genetic distances (Table 4) and the resulting dendrogram (Fig. 2). (Note that the genetic distance (D) values are calculated from variable loci only, and that some of the loci may be affected by natural selection. Thus, D is only used as a convenient measure of the amount of allelic divergence at this particular set of loci. Similarly, the dendrogram depicts nothing but a convenient graphical representation of genetic similarity at this set of loci among samples from different geographic regions.) The largest genetic distances (about 0.01) involve comparisons including the Baltic sample. This distance value is very low considering the samples being collected over most of the range of the species; nevertheless the distances are inflated because only variable loci were included in the calculation of genetic distances. The major observations from the dendrogram include (1) the distinct separation of sample I (Baltic Sea) from the remaining samples and (2) the distinct subclustering of samples from the eastern and western Atlantic Ocean, respectively.

TABLE 3. Frequencies of variant alleles at the 13 loci variable in the present study (cf. Table 1; Fig. 1). The estimates of average heterozygosity ($\bar{H}$) are based on 19 and 10 loci, respectively (see text for further explanation). Allele frequency homogeneities were tested by the *G*-statistic using William's correction for small expected values (Sokal and Rohlf 1981). *n* = number of fish analyzed; df = degrees of freedom; NS = nonsignificant; $*P < 0.05$; $***P < 0.001$.

Locus and allele	Sample									*G*	df	Sign.
	A	B	C	D	E	F	G	H	I			
AAT-2												
−50	0	—	0	—	—	0	0.018	0	—	7.80	4	NS
n	97	—	100	—	—	96	85	100	—			
CK-1												
85	0	0.005	0	0	0	0	0	0	0	3.32	8	NS
105	0	0	0	0	0.005	0	0	0	0			
n	97	96	100	96	96	96	100	100	98			
G3P-1												
−300	0	0.005	0	0	0	0	0	0	0.005	12.55	8	NS
−100	0.010	0.010	0.020	0.028	0.012	0.010	0.045	0.030	0.026			
200	0	0	0	0	0	0.005	0.015	0	0			
n	97	96	100	18	83	96	99	100	98			
IDH-1												
140	0.132	0.124	0.115	0.097	0.163	0.130	0.194	0.138	0.194	12.95	8	NS
n	95	93	100	72	86	96	98	94	93			
IDH-2												
50	0	0	0	0	0	0	0.005	0	0	16.80	8	*
200	0.005	0	0.005	0.027	0.016	0	0.005	0	0			
n	97	94	100	92	96	95	97	100	99			
LDH-2												
95	0	0	0.005	0	0	0	0	0	0	1.63	8	NS
n	97	96	100	96	96	96	100	100	99			
LDH-3												
70	0.366	0.411	0.445	0.422	0.370	0.385	0.380	0.415	0.152	58.54	8	***
85	0	0	0	0	0	0.005	0	0	0			
140	0	0	0	0.010	0.016	0.021	0	0	0			
n	97	96	100	96	96	96	100	100	99			
MDH-3												
60	0.005	0	0	0	0	0.016	0.015	0.011	0	13.44	8	NS
n	97	96	100	96	96	96	100	100	99			
MP												
90	0.005	0.010	0.005	0	—	0	0.011	0	0	6.76	7	NS
n	97	96	100	63	—	96	100	100	99			
PGI-1												
65	0	0.021	0.030	0.023	0.021	0.026	0.025	0.035	0.005	35.31	8	***
97	0	0	0	0	0	0	0	0	0.031			
135	0.531	0.464	0.350	0.351	0.292	0.307	0.300	0.303	0.316			
160	0.010	0	0	0	0	0	0	0	0			
n	97	96	100	87	96	96	100	99	98			
PGI-2												
90	0	0	0	0.016	0.011	0.010	0	0	0	12.92	8	NS
n	97	96	100	96	95	96	100	100	99			
PGM-1												
70	0	0	0	0	0.005	0	0	0.005	0	6.10	8	NS
80	0.021	0.021	0.015	0.006	0.016	0.026	0.020	0.015	0			
120	0	0	0.005	0	0.005	0	0.005	0	0.005			
n	97	95	99	83	93	96	100	98	99			
SDH-1												
−100	0	—	0	—	—	0	0	0.005	0	1.37	5	NS
n	97	—	100	—	—	96	85	98	31			
$\bar{H}$ (19 loci), %	6.97		6.83			6.97	7.93	6.95				
$\bar{H}$ (10 loci), %	12.81	13.02	12.88	13.09	13.38	13.24	14.52	13.10	11.20			

TABLE 4. Geographic distances (km; below diagonal) and genetic distances (Nei 1972) calculated from 10 variable loci (above diagonal) among samples of Atlantic cod. The average genetic distance between each of the nine samples and the other eight ones is given in the rightmost column.

	Sample	A	B	C	D	E	F	G	H	I	Average
A	North America		0.00073	0.00420	0.00423	0.00654	0.00563	0.00653	0.00578	0.01046	0.00551
B	Greenland	3346		0.00154	0.00172	0.00379	0.00286	0.00392	0.00281	0.01057	0.00349
C	Iceland	5423	2154		0.00020	0.00132	0.00062	0.00167	0.00043	0.01072	0.00259
D	Barents Sea	8000	4846	2577		0.00129	0.00064	0.00184	0.00058	0.00997	0.00256
E	Malangen	7615	4346	2192	885		0.00029	0.00040	0.00041	0.00619	0.00253
F	Trondheimsfjorden	7077	3808	1654	1923	1038		0.00076	0.00015	0.00761	0.00233
G	Oslofjorden	7692	4423	2269	2923	2346	1346		0.00059	0.00611	0.00273
H	North Sea	7461	4192	2038	2961	2500	1500	1077		0.00838	0.00239
I	Baltic Sea	8307	5038	2885	3692	2885	1961	769	1654		0.00875

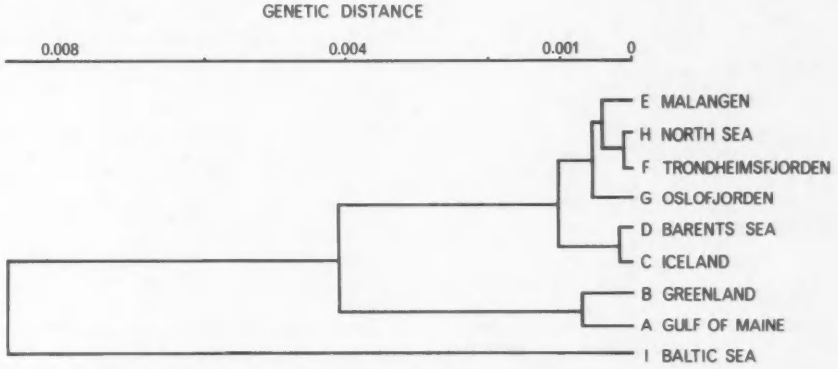

FIG. 2. Dendrogram (UPGM; Sneath and Sokal 1973) constructed from pairwise genetic distances calculated from 10 variable electrophoretic loci (cf. Table 4).

Population Structure of Atlantic Cod

Our results indicate that the genetic differentiation of Atlantic cod is weak. This characteristic is particularly reflected in the very low genetic distance between the most diverged samples (0.011), and the small fraction of the total gene diversity being explained by differences among samples (2.1%). These characteristics persist amidst the clear divergence of the Baltic Sea sample, and the apparent distinction of the samples from the eastern and western Atlantic Ocean, respectively. Considering the possibility of natural selection affecting the genotypic distributions of the two most variable loci (*LDH-3* and *PGI-1*; cf. Mork and Sundnes 1985b) does not alter the impression of a generally small amount of genetic differentiation among the populations sampled. Although we lack information on the type of selection that may occur, it is reasonable to assume that environmental heterogeneity among locations would tend to amplify allele frequency differences at selected loci and, thus, inflate the estimates of genetic divergence.

Under a neutral model the low amount of genetic differentiation may be explained in two different ways: either as a result of the recent divergence of large populations, or as a result of a substantial gene flow between stocks. The latter explanation has considerable independent support. Evidence from tagging experiments (see the introduction) indicates that considerable migration occurs between stocks. Recent experiments demonstrating successful voluntary interstock matings (Jørstad et al. 1983) also indicate an absence of absolute reproductive barriers.

The possibility of gene flow as a major explanatory cause for the observed allelic distributions was examined by comparing the geographic and genetic distances (Table 4; Fig. 3) (note that all observations are not independent). The correlation between corresponding values in the two matrices, which was significant using all 36 pairwise combinations of locations ($r = 0.483$, $P = 0.003$), was greatly increased by excluding the Baltic Sea sample ($r = 0.916$, $P \ll 0.001$), with as much as 84% (r^2) of the variation in genetic distance being explained by geographic distance. This high correlation is compatible with a model of distance-dependent gene flow (isolation by distance) among groups of cod in the Atlantic Ocean.

In contrast, the distinct nature of the Baltic Sea sample is more consistent with a model implying restricted gene flow between the Baltic Sea and the Atlantic Ocean. It could be that the Baltic population experienced an initial population bottleneck followed by continued isolation due, perhaps, to ecological barriers such as salinity differences. The observation of the highest average genetic distance from other samples and the largest difference in heterozygosity between the adjacent Baltic Sea and Oslofjorden samples (with the lowest value in the Baltic Sea sample which also had fewer alleles segregating; Table 3) is consistent with such a bottleneck event. However, if the colonization of the Baltic Sea was in fact associated with a population size reduction, it appears that the bottleneck did not persist for a very long time. The very small amount of divergence from the Atlantic stocks and the quite modest reduction of average heterozygosity indicate that genetic drift did not affect the population over extended periods of time. We stress that an absolutely small amount of electrophoretically

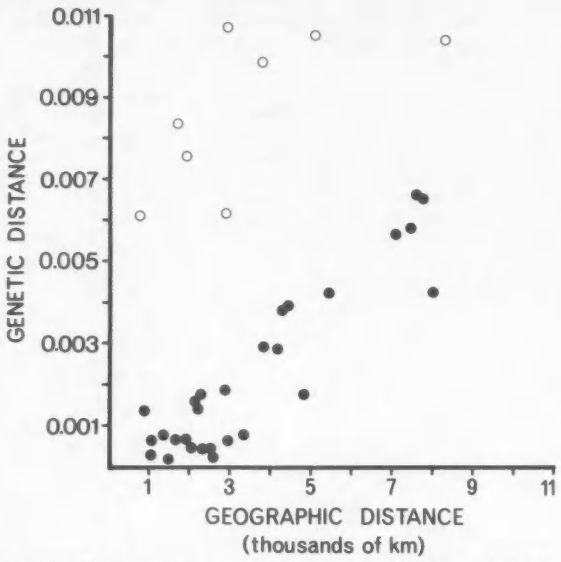

FIG. 3. Relation between geographic and genetic distances in Atlantic cod. The eight values involving Baltic Sea are marked as open circles.

detectable divergence may well be associated with substantial morphologic differentiation (Lewontin 1984). The statistical test procedures applicable to morphologic characters frequently have a higher statistical power than tests for allele frequency differences (Lewontin 1984), and this is true regardless of the cause of the morphologic differences (i.e. environmental heterogeneity or genetic differentiation at the loci affecting the morphologic character). Thus, there is no conflict between, for example, our present results and those of Svetovidov (1948) who reported conspicuous morphological differences between the cod of the Baltic Sea and that of the Atlantic Ocean.

Systematic Considerations

Clearly, the systematic implications of our results are that the Atlantic cod appears to be a single species with apparently sufficient gene flow to prevent substantial genetic divergence over rather extended geographic regions throughout the Atlantic Ocean. The somewhat differentiated Baltic Sea population after all exhibits very little genetic divergence from the Atlantic stocks. This stock structure is similar to that of the Pacific cod, *Gadus macrocephalus* (Grant, in press), in which only slightly diverged population groups were found in the eastern and western Pacific Ocean. These patterns were also observed in several other marine species such as Pacific herring (*Clupea pallasi*) and Atlantic herring (*C. harengus*) (Grant 1984; Grant and Utter 1984; Ryman et al. 1984), Pacific halibut (*Hippoglossus stenolepis*) (Grant et al. 1984), and walleye pollock (*Theragra chalcogramma*) (Grant and Utter 1980), where large population sizes coupled with some degree of gene flow have also apparently prevented substantial genetic divergence among stocks over broad geographic areas. This common observation of little divergence among stocks of marine species has recently been discussed by Gyllensten (1985) relative to the genetic variability pattern typical for anadromous and freshwater populations of fishes.

Our findings differ from those of other investigators using similar, but less extensive data. Some of the inconsistencies result from questionable interpretations of raw data (discussed by Shaklee 1983) or focusing entirely on a single or a few loci, some of which may to a considerable degree be subjected to natural selection (e.g. haemoglobin, see Mork et al. 1983, 1984a, 1984b; Mork and Sundnes 1984, 1985a). Allele frequency differences at a locus that is influenced by selective forces may be helpful when identifying groups of fish that have experienced similar environmental conditions; in that respect, such a locus may provide significant information relative to the management of various stock segments. It is important to recognize, however, that allele frequency differences at such loci do not necessarily imply that the various groups represent offspring from reproductively distinct populations.

One recent publication (Jørstad 1984) presented data confirming our findings of a general lack of apparent allele frequency heterogeneity among stocks of cod from the Atlantic Ocean: allele frequency data for *LDH-3* and *PGI-1* are reported for cod in Northern Norway and are similar to ours from that region, but the conclusions are quite different. Jørstad (1984) stated that his findings reflect "... the existence of several genetically differentiated groups. ..." However, many of the differences are not statistically significant (in contrast with what is claimed in the paper). Further, the statistical tests are based on genotypic distributions whereas only allele frequencies are presented. Populations are characterized by allele frequencies whereas differences in genotypic proportions may reflect nothing but, for example, local differences in mating patterns (cf. Nei 1973b, 1975).

Our findings do not represent the final revelation of the genetic structure of Atlantic cod. For example, a more thorough understanding of the apparent genetic distinction of the Baltic cod requires further insights based on additional samples, as well as a broader sampling of the genome through analysis of additional protein loci and examination of potential differences at the DNA level (Berg and Ferris 1984). However, our findings have considerable immediate significance through identifying major population units, providing a basis for further investigations, and clarifying past systematic misconceptions.

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Relationship Between Nutrients, Dominant Ions, and Phytoplankton Standing Crop in Prairie Saline Lakes

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Bierhuizen, J. F. H., and E. E. Prepas. 1985. Relationship between nutrients, dominant ions, and phytoplankton standing crop in prairie saline lakes. Can. J. Fish. Aquat. Sci. 42: 1588–1594.

We collected data from 20 saline lakes (total dissolved solids from 1000 to 91 000 $mg \cdot L^{-1}$) in southeastern Alberta to compare relationships between phosphorus, nitrogen, and phytoplankton standing crop with those in freshwater lakes. In 18 lakes, Na^+, Mg^{2+}, SO_4^{2-}, and HCO_3^--CO_3^{2-} were the dominant ions. In these lakes there was a significant positive correlation between Ca^{2+} and chlorophyll *a* (Chl *a*), and there were significant negative correlations between Chl *a* and conductivity, pH, Na^+, Mg^{2+}, SO_4^{2-}, HCO_3^-, and CO_3^{2-}. When all 20 lakes were considered there were no significant relationships between Chl *a* and phosphorus or nitrogen. Empirical relationships for freshwater lakes, based on spring or summer total phosphorus (TP) or total nitrogen (TN), overestimated Chl *a* in all the study lakes. However, in saline lakes with similar ionic composition and TN to TP ratios greater than 12 (by weight), there was a significant positive relationship between TP and Chl *a*. For the saline lakes with TN to TP ratios greater than 12, the deviations between the Chl *a* levels predicted from models developed for freshwater lakes and the observed levels were positively correlated with conductivity, total dissolved solids, and Na^+ ($r^2 = 0.78$–0.82, $P < 0.001$). We developed the first empirical model that describes nutrient – Chl *a* relationships for inland saline lakes. The deviation of measured phytoplankton biomass from that predicted by models developed for freshwater lakes can be explained by conductivity or dominant ion concentration.

Les auteurs ont recueilli des données dans 20 lacs salés (total des solides dissous variant de 1 000 à 91 000 $mg \cdot L^{-1}$) du sud-est de l'Alberta afin de comparer les relations entre le phosphore, l'azote et la biomasse phytoplanctonique avec celles des lacs d'eau douce. Dans 18 lacs, Na^+, Mg^{+2}, SO_4^{-2}, HCO_3^--CO_3^{-2} représentaient les ions dominants et il existait une corrélation positive significative entre Ca^{+2} et la chlorophylle *a* (Chl *a*) et des corrélations négatives significatives entre Chl *a* et la conductivité, le pH, Na^+, Mg^{+2}, SO_4^{-2}, HCO_3^- et CO_3^{-2}. Quand les 20 lacs étaient considérés, il n'y avait aucune relation significative entre Chl *a* et le phosphore ou l'azote. Les relations empiriques pour les lacs d'eau douce, basées sur le phosphore total (PT) ou l'azote total (NT) présents au printemps ou en été, surestimaient Chl *a* dans tous les lacs expérimentaux. Toutefois, dans les lacs salés dont la composition ionique était semblable et les rapports entre le NT et le PT dépassaient 12 (en poids), il existait une relation positive significative entre le PT et Chl *a*. Dans les lacs salés où les rapports entre le NT et le PT étaient supérieurs à 12, les écarts entre les taux de Chl *a* prédits selon les modèles élaborés pour les lacs d'eau douce et les taux observés étaient en corrélation positive avec la conductivité, les solides dissous totaux et Na^+ ($r^2 = 0{,}78$–$0{,}82$, $P < 0{,}001$). Les auteurs ont créé le premier modèle empirique qui décrit les relations entre les bioéléments et Chl *a* dans les lacs salés intérieurs. La conductivité ou la concentration de l'ion dominant peut expliquer l'écart entre la biomasse phytoplanctonique quantifiée et celle prédite selon des modèles mis au point pour des lacs d'eau douce.

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Primary production in some saline lakes can be substantially higher than the rates reported for freshwater eutrophic lakes (Wetzel 1964; Walker 1973; Haynes and Hammer 1978; Melack 1979; Wetzel 1983). However, high salinity levels appear to depress (1) the number of benthic organisms (Rawson and Moore 1944), (2) maximum summer chlorophyll *a* (Chl *a*) levels as compared with less saline lakes (Barica 1978), and (3) Chl *a* to total phosphorus (TP) ratios as compared with freshwater lakes (Prepas and Trew 1983). Thus, the literature on productivity in saline lakes does not indicate clear overall patterns nor does it indicate whether the established empirical relationships for freshwaters (Ryder 1965; Sakamoto 1966; Nicholls and Dillon 1978; Smith 1982; Hanson and Leggett 1982; Prepas and Trew 1983) apply to saline lakes. In saline lakes the ionic composition can vary substantially, even within a small geographical area (Rawson and Moore 1944; Barica 1978; Hammer 1978; Gorham et al. 1983). However, the effect of ionic composition and salinity on lake productivity has not been investigated.

To evaluate the relationship between ionic composition, salinity, nutrients, and phytoplankton standing crop in prairie saline lakes, we sampled 20 lakes in southeastern Alberta from May to August 1983. For lakes with similar ionic composition, chemical characteristics were tested for significant correlations with Chl *a*. The relationships between nutrients and Chl *a* in these saline lakes were then compared with empirical models developed for freshwater lakes to determine whether Chl *a* – nutrient relationships for saline lakes were different from those reported for freshwater lakes.

The boundary between fresh and saline waters based on

ecological criteria has yet to be established. Total dissolved solids (TDS) content is routinely used to define saline lakes; the boundary can range from 300 mg·L^{-1} (Rawson and Moore 1944) to 5000 mg·L^{-1} (Beadle 1981). An arbitrary boundary of 3000 mg TDS·L^{-1} (Williams 1964, 1981a) is commonly used. Freshwater species are routinely found in waters with less than 1000 mg TDS·L^{-1}, whereas few freshwater species are found in water with more than 10 000 mg TDS·L^{-1} (Beadle 1969; Williams 1981b). In addition, Prepas and Trew (1983) noted that ratios of Chl *a* to TP were lower in lakes with more than 700 mg TDS·L^{-1} than in lakes containing less than 700 mg TDS·L^{-1}. Because the boundary between fresh and saline waters is unclear, based on biological criteria, we chose a boundary that separated lakes with freshwater species and standard ratios of Chl *a* to TP (Dillon and Rigler 1974) from lakes with salt-tolerant species and apparently lower ratios of Chl *a* to TP (Prepas and Trew 1983), i.e. 1000 mg·L^{-1}.

Materials and Methods

The saline lakes were sampled every 3 wk from May to August 1983. On each visit, vertical profiles of temperature and light were measured at the deepest site in the lake (see Table 1). Temperature was measured at 1-m intervals with a resistance thermistor accurate to 0.1°C. The bottom of the trophogenic zone was defined as the depth at which there was 1% of surface light as measured with a Protomatic photometer (Protomatic, Dexter, MI) or twice the Secchi disc reading. The Protomatic photometer, which measures irradiance between 300 and 800 nm, and a LiCor L1-185 light meter with a quantum sensor, which measures photosynthetically active radiation, gave the same depths for the trophogenic zone. In each lake, integrated samples from the trophogenic zone were collected with weighted Tygon tubing at three to five stations (dependent on lake size) and pooled. When the trophogenic zone extended to within 0.7 m of the lake bottom or deeper, samples were collected to a depth of 0.7 m above the lake sediments. In the very turbid, shallow lakes with a trophogenic zone less than 0.5 m deep, a 1.5-L aluminum drop-sleeve water bottle was used to collect surface water samples.

Duplicate, integrated water samples for NH_4^+ and total Kjeldahl nitrogen (TKN) analyses were placed in 250-mL polystyrene containers; samples for TKN were acidified with 0.25 mL of concentrated sulfuric acid within 1 h of collection. A 1-L Nalgene polyethylene bottle was used to store samples for NO_2^- and NO_3^- analyses. Duplicate, integrated water samples for TP, total dissolved phosphorus (TDP), total Fe, SO_4^{2-}, Cl^-, alkalinity, conductivity, TDS, pH, Na^+, K^+, Ca^{2+}, Mg^{2+}, color, turbidity, and Chl *a* analyses were placed in Nalgene polyethylene bottles (opaque bottles were used for Chl *a* samples), which were completely filled. All water samples were stored on ice in coolers and then refrigerated at 4°C in the laboratory until they were analyzed. Within 10 h of collection, water samples for TP, TDP, and Chl *a* were filtered under low pressure (−50 kPa). Samples for TP analyses were prefiltered through a 250-μm Nitex net and transferred to culture tubes (after Prepas and Rigler 1982). Samples for TDP analyses were filtered through prewashed 0.45-μm HAWP Millipore membrane filters and transferred to culture tubes. Samples for Chl *a* analyses were filtered through Whatman GF/C filters. The filters were placed in petri dishes, wrapped in aluminum foil, and stored on ice or in a freezer. Samples for nitrogen and dissolved oxygen (DO) analyses were processed within 9 to 48 h of collection. Analyses for Na^+, K^+, Ca^{2+}, and Mg^{2+} were conducted within 10 d of collection, the remaining analyses within 6 d. The containers for nitrogen analyses were cleaned with double-distilled water (DDW) only; all other containers were acid-washed in 2% HCl and rinsed with DDW.

Ammonium and TKN were analyzed by Solorzano's (1969) phenolhypochlorite method as modified by Prepas and Trew (1983). Nitrate and nitrite were determined, after filtration through a prewashed 0.45-μm HAWP Millipore membrane filter, by the cadmium–copper reduction method of Stainton et al. (1977). Ammonium analyses were performed in triplicate; all other nitrogen samples in duplicate. Total nitrogen (TN) was calculated as the sum of TKN, NO_3^-, and NO_2^-.

Total and dissolved phosphorus samples were digested and analyzed by Menzel and Corwin's (1965) potassium persulfate method. Total Fe was determined by the phenanthroline method (American Public Health Association 1975). Water samples for SO_4^{2-} analyses were filtered through a prewashed Whatman GF/C filter and analyzed by the gravimetric method with ignition of the residue (American Public Health Association 1975). Alkalinity was determined by the potentiometric titration method (Environment Canada 1979). A Fisher Accumet digital pH meter was used to measure pH and to determine the end points for the alkalinity titration. Samples for Na^+, K^+, Ca^{2+}, and Mg^{2+} analyses were filtered through a prewashed Whatman GF/C filter, stored at 4°C, and analyzed by flame emission on a Jarrel Ash (model JA 82-270) or Varian (model AA6) atomic absorption flame emission spectrophotometer (American Public Health Association 1975). No lanthanum was added to the water samples for Ca^{2+} and Mg^{2+} analyses. Chemical interference caused by silicate, carbonate, and phosphorus was overcome with a nitrous oxide – acetylene flame (Stainton et al. 1977; Environment Canada 1979). Interference by ionization could not be reduced by lanthanum (American Public Health Association 1975; Environment Canada 1979); addition of lanthanum caused formation of a white precipitate. Ionization interference can also be overcome by potassium (Environment Canada 1979); potassium levels were greater than 18 mg·L^{-1} in our samples, which should prevent ionization interference.

Conductivity was measured with a YSI model 31 conductivity bridge on water samples at 20°C. Standard KCl solutions, with concentrations ranging from 0.5 to 100 g·L^{-1}, were used to test the linearity of the conductivity bridge. The conductivity–KCl relationship was linear up to 20 g KCl·L^{-1} ($n = 8$, $r^2 = 1.00$, $P < 0.0001$). At KCl concentrations greater than 20 g·L^{-1}, there was also a significant positive relationship, although the slope was lower (*t*-test, $P < 0.001$). Since water from Oliva Lake had a conductivity greater than the 20 g KCl·L^{-1} standard, the mean conductivity value for this lake was corrected (from 48 560 to 57 812 μS·cm^{-1}).

Samples for TDS were filtered through a prewashed 0.45-μm HAWP Millipore membrane filter and dried at 103°C (Stainton et al. 1977). Color was measured on centrifuged samples with the platinum–cobalt method on a Hellige-Aqua Tester (model 611-A). Turbidity was measured with a Hach Turbidimeter (model 2100A). Dissolved oxygen was determined in all lakes, except Oliva and Birch, according to Carpenter's (1965) modified Winkler technique. To avoid effervescence of the water samples from Oliva and Birch lakes, the Miller method for DO (Walker et al. 1970) was also used. Chlorophyll *a* was determined in triplicate with a spectrophotometric technique based upon the ethanol extraction procedure of M. Ostrovsky (Biology Department, Alleghany College, Meadville, PA, unpubl.)

TABLE 1. Background data for the 20 study lakes: location, surface area (area), maximum depth (z), pH, color, total dissolved solids (TDS), turbidity, conductivity, and total iron. The chemical data are averages for the trophogenic zone in 1983.

	Coordinates		Area	z	Conductivity	TDS		Total iron	Color	Turbidity
	(°N)	(°W)	(km^2)	(m)	($\mu S \cdot cm^{-1}$)	($mg \cdot L^{-1}$)	pH	($\mu g \cdot L^{-1}$)	($mg\ Pt \cdot L^{-1}$)	(JTU)
Oliva	53°05′	111°36′	0.5	1.7	57 812[a]	90 728[b]	10.1	556	36	2
Birch	53°21′	111°32′	4.5	3.0	16 848	15 052	9.6	1714	54	22
Peninsula	52°52′	111°29′	1.4	3.1	11 380	9 600	9.3	1454	43	13
Red Deer	52°44′	113°06′	18	7.5	10 283	8 250	9.4	562	14	6
Fluevog	52°50′	111°19′	0.3	2.1	8 456	8 400	9.2	2124	92	15
Miquelon	53°15′	112°55′	7.8	4.0	6 530	5 402	9.4	109	10	9
White's	53°21′	111°39′	4.0	1.5	5 118	3 432	9.2	3834	117	47
Haunted	52°25′	113°10′	2.2	2.7	2 818	2 072	9.7	395	34	4
Joseph	53°17′	113°04′	5.9	3.0	2 753	2 026	9.1	400	21	9
Wappa	53°22′	111°37′	1.0	2.0	2 635	1 756	9.0	3797	107	47
Buffalo east	52°30′	112°52′	51	7.0	2 433	1 806	9.2	91	8	3
Buffalo middle	52°27′	112°58′	22	3.0	1 993	1 334	9.2	195	17	7
Postill	52°14′	112°54′	0.9	0.9	1 735	1 340	8.9	631	86	10
Camp	53°05′	111°32′	1.4	4.0	1 663	1 214	9.2	59	28	14
Buffalo west	52°27′	113°01′	4.1	2.3	1 446	1 022	9.2	165	34	8
Cooking east	53°26′	113°01′	11	3.6	1 445	1 058	8.9	163	38	13
Looking back	53°19′	113°09′	2.8	2.0	1 406	1 001	8.9	158	54	14
Cooking west	53°25′	113°05′	19	2.6	1 360	979	8.9	198	40	14
Mink north	53°31′	114°14′	0.4	7.0	1 324	1 211	8.3	21	5	2
Mink south	53°31′	114°14′	0.6	8.0	1 311	1 111	8.3	25	5	1

[a]Value recalculated as in text.
[b]Average summer value.

described by Bergmann and Peters (1980). The ethanol extraction method gives values that are not statistically different from Yentsch and Menzel's (1963) acetone extraction technique, which corrects for phaeophytin (Prepas 1984).

In most cases, samples were diluted with DDW after filtration and prior to analysis to ensure that they would be within the range of the methods employed. Spring and summer values were defined as in Prepas and Trew (1983). Spring samples were collected for all study lakes except for Postill and Buffalo west.

To estimate empirical relationships, we used linear regression analyses on mean values. A logarithmic transformation (base 10) was applied to all data. The transformed data approached a normal distribution. Empirical relationships were calculated with the BMDP statistical software package (Dixon 1981).

Results

Description of Lakes

The lakes are located between 52°14′–53°31′N and 111°19′–114°14′W, centered 160 km southeast of Edmonton, Alta., in the Aspen Parkland region of Alberta (Strong and Leggat 1981). The climate is continental; the mean annual precipitation is 300–450 mm and the mean annual lake evaporation is 600–700 mm (Fisheries and Environment Canada 1978). The area varies from undulating relief to rolling hills. The soil type in the study area is predominantly black Chernozem; saline soils are near some of the lakes (Wyatt et al. 1944; Bowser et al. 1947, 1962).

The lakes range in surface area from 0.3 to 51 km^2 and in maximum depth from 0.9 to 8 m. During summer 1983, none of the lakes was thermally stratified. Conductivity ranged from 1311 to 57 812 $\mu S \cdot cm^{-1}$; only water from Oliva Lake was above 20 000 $\mu S \cdot cm^{-1}$. The pH varied from 8.3 to 10.1 and total iron from 0.021 to 3.8 $mg \cdot L^{-1}$. Only two lakes were turbid (>25 JTU) and highly colored (>107 mg $Pt \cdot L^{-1}$) (Table 1). Two lakes, Cooking and Mink, are double-basined and one lake, Buffalo, has three basins. The basins are treated as separate lakes for data analyses because there were differences between basins (Tables 1, 2).

The average concentrations of the major ions in the trophogenic zone of the study lakes are summarized in Table 2. The average concentrations of K^+, Ca^{2+}, Mg^{2+}, and Cl^- varied less than those of Na^+, SO_4^{2-}, HCO_3^-, and CO_3^{2-}; the former group varied from 4 to 515 $mg \cdot L^{-1}$ and the latter from undetectable to 29 000 $mg \cdot L^{-1}$. For all lakes except Oliva, the difference in positive and negative charges expressed as total milliequivalents of anions per litre and total milliequivalents of cations per litre over the sum of milliequivalents of anions and cations was less than 7%; for Oliva Lake the difference was 16%. There was a strong correlation between total ion concentration, [TI] (milligrams per litre), and TDS concentration (milligrams per litre) for 19 lakes (excluding Oliva Lake):

$$(1)\quad [TDS] = 28.7 + 0.91 \cdot [TI] \qquad (n = 19,\ r^2 = 0.99,\ P < 0.0001).$$

The slope of Eq. 1 was not significantly different from unity (t-test, $P > 0.4$). In these 19 lakes the cation–anion balance and the strong relationship between TI and TDS indicate that most of the ions were accounted for. Eighteen of the 20 study lakes had a similar ionic composition (percent milliequivalents) with Na^+ (and Mg^{2+} in the mildly saline lakes), CO_3^{2-}, HCO_3^-, and SO_4^{2-} as the dominant ions. Water from Mink north and south was dominated by Mg^{2+}, Ca^{2+}, and SO_4^{2-}; consequently, these lakes were excluded from the relationships between dominant ions, nutrients, and Chl a.

TABLE 2. Average concentration ($mg \cdot L^{-1}$) of the major ions. The data are average concentrations in the trophogenic zone over the spring and summer 1983 in the 20 saline lakes in Alberta (ND = not detectable).

	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}	HCO_3^-	CO_3^{2-}
Oliva	22 765	421	16	139	515	29 422	4462	21 142
Birch	5 232	134	18	66	319	6 645	2376	2 189
Peninsula	3 363	109	28	107	178	4 842	1416	694
Red Deer	2 745	72	17	146	69	4 426	1144	637
Fluevog	2 304	66	26	59	142	2 645	1480	564
Miquelon	1 473	110	14	206	99	2 413	888	517
White's	1 282	47	23	27	64	1 511	984	333
Haunted	684	37	11	44	28	231	762	596
Joseph	596	64	25	48	36	628	671	165
Wappa	606	26	31	28	18	660	667	150
Buffalo east	502	45	14	86	13	398	756	225
Buffalo middle	392	36	20	74	14	314	680	180
Postill	318	41	76	38	20	436	420	79
Camp	307	36	16	91	11	239	579	224
Buffalo west	276	26	25	57	9	220	155	445
Cooking east	244	46	30	50	17	334	355	71
Looking back	251	32	36	27	138	216	227	61
Cooking west	233	43	30	48	16	304	333	69
Mink north[a]	51	19	127	108	5	654	141	ND
Mink south[b]	52	22	126	106	4	647	145	ND

[a]Average concentration excluding August 23 samples.

TABLE 3. Nutrient and Chl *a* analyses ($\mu g \cdot L^{-1}$) for the 20 saline lakes in Alberta.

	Spring		Mean summer					
	TP	Chl *a*	TP	TDP	TN	$(NO_2^- + NO_3^-)$-N	NH_4^+-N	TN:TP
Oliva	11 285	7.0	14 077	13 438	10 736	3	285	0.8
Birch	10 642	18.6	13 533	13 389	6 096	34	82	0.5
Peninsula	3 422	6.7	3 513	3 432	4 696	38	62	1.3
Red Deer	961	4.5	1 026	972	3 919	19	38	3.9
Fluevog	2 131	4.1	2 213	2 144	4 441	38	56	1.9
Miquelon	122	3.5	132	109	6 160	3	20	44
White's	3 902	6.9	4 223	4 050	3 890	36	50	0.9
Haunted	119	5.9	69.9	47.8	4 997	1	18	68
Joseph	337	33.7	288	222	5 615	7	208	18
Wappa	1 182	30.2	1 406	1 354	3 563	30	59	2.5
Buffalo east	45.6	6.7	53.0	32.8	2 886	3	27	56
Buffalo middle	54.3	11.2	71.1	31.5	2 785	2	21	41
Postill	—	62.0	2 620	2 426	6 248	26	249	2.4
Camp	157	45.6	188	58.2	4 490	8	30	24
Buffalo west	—	7.8	63.5	24.9	2 403	2	24	41
Cooking east	171	84.1	225	60.6	6 924	3	35	29
Looking back	294	85.7	288	71.1	6 699	7	30	21
Cooking west	192	90.0	260	57.0	6 884	4	37	25
Mink north	32.8	5.0	23.0	—	1 094	4	8	45
Mink south	27.7	5.0	20.9	—	1 103	1	6	50

Nutrient–Chlorophyll Relationships

In the 20 saline lakes, mean summer Chl *a* in the trophogenic zone ranged from 4 to 90 $\mu g \cdot L^{-1}$ and mean summer TP ranged from 21 to 14 077 $\mu g \cdot L^{-1}$. In these lakes the ratio of TDP to TP varied from 22 to 96%. The median ratio, however, is 87%, which indicates that in most of these lakes TP was dissolved and could be available for algal and bacterial production. The variation in the nitrogen values was less extreme than for phosphorus; summer TN ranged from 1094 to 10 736 $\mu g \cdot L^{-1}$. The ratio of TN to TP varied from 0.5 to 68 (Table 3).

For the 18 lakes with similar ionic composition, correlations between summer Chl *a* and nutrients, i.e. spring TP, summer TP, summer TDP, summer TN, summer $NO_3^- + NO_2^-$, and summer NH_4^+, were not significant ($P > 0.14$). However, when only the lakes with a ratio of TN to TP greater than 12 were considered, there was a significant positive relationship between summer TP and summer Chl *a* ($n = 10$, $r^2 = 0.68$, $P < 0.004$). The summer TP and summer Chl *a* data for these 10 saline lakes were compared with Prepas and Trew's (1983) data for freshwater lakes in the same region. Prepas and Trew's empirical TP – Chl *a* model, which includes five saline lakes, was recalculated

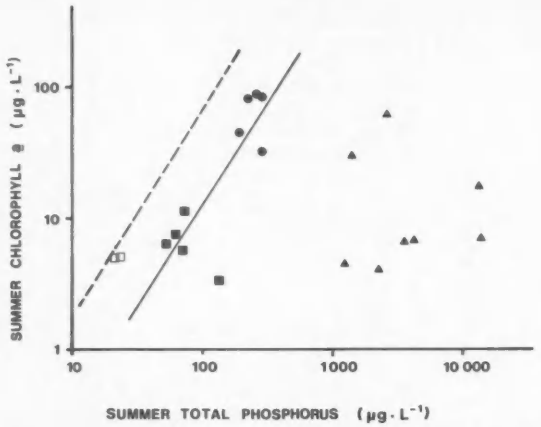

FIG. 1. Relationships between summer TP and Chl *a* ($\mu g \cdot L^{-1}$) for 20 saline lakes in central Alberta. The solid line is the linear regression of summer Chl *a* on summer TP for lakes with similar ionic composition and a TN to TP ratio greater than 12. The broken line is the linear regression of summer Chl *a* on summer TP for freshwater lakes in the same region (Prepas and Trew 1983). □, Mink Lake; ▲, lakes with TN:TP < 12; ●, lakes with TN:TP between 12 and 35; ■, lakes with TN:TP > 35.

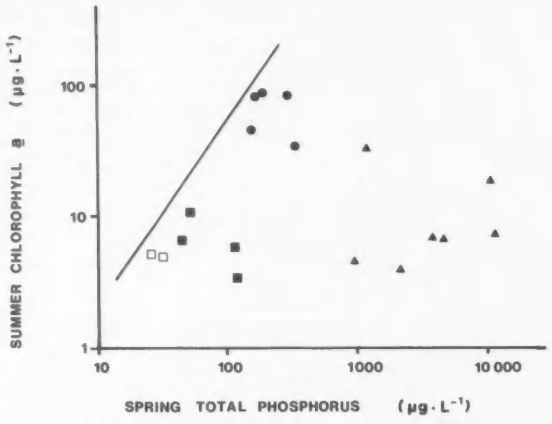

FIG. 2. Relationship between spring TP and summer Chl *a* ($\mu g \cdot L^{-1}$) for 18 saline lakes in central Alberta. The solid line is the Dillon and Rigler's (1974) empirical model for freshwater lakes. Symbol designations are as in Fig. 1.

to include only freshwater lakes ($n = 27$, $r^2 = 0.86$, $P < 0.0001$). Our saline lakes are all below the recalculated regression line (Fig. 1).

There were no significant correlations between spring TP and summer Chl *a*, although when only lakes with a ratio of TN to TP greater than 12 were considered, the relationship was almost significant ($P = 0.054$). When the spring TP – summer Chl *a* data from our saline lakes were compared with Dillon and Rigler's (1974) TP – Chl *a* model, including those with a TN to TP ratio greater than 12, all fell below the line (Fig. 2). The deviations between predicted and observed Chl *a* values were greater for the more saline lakes.

Lakes with a ratio of TN to TP less than 12 form a distinct group (Fig. 1, 2), with high spring TP (range 961 – 11 285 $\mu g \cdot L^{-1}$) and summer TP (range 1026 – 14 077 $\mu g \cdot L^{-1}$) and for these TP levels remarkably low summer Chl *a* (range 4–62 $\mu g \cdot L^{-1}$). The relationships between summer Chl *a* and nitrogen and phosphorus were far from significant ($P > 0.22$) in the eight lakes where the ratio of TN to TP was less than 12. Therefore, in these saline lakes, the influence of nitrogen and phosphorus on phytoplankton standing crop is very different from freshwater systems.

Average total iron ranged from 0.02 to 3.80 $mg \cdot L^{-1}$ (Table 1). No correlation was found between total iron and summer Chl *a* in lakes with a similar ionic composition ($n = 18$, $P > 0.35$). Since the surface water of all lakes except Oliva Lake was well oxygenated (>10 mg $DO \cdot L^{-1}$) and TP levels were extremely high, iron could have been bound to TP and thus unavailable to phytoplankton (Huntsman and Sunda 1980).

Dominant Ion – Chlorophyll Relationships

In lakes with similar ionic composition ($n = 18$), significant correlations were found between summer Chl *a* and the following variables: conductivity, pH, Na^+, Ca^{2+}, Mg^{2+}, SO_4^{2-}, HCO_3^-, and CO_3^{2-} (Table 4). The Ca^{2+}–Chl *a* relationship was positive; the remaining relationships were negative. Chlorophyll *a* levels were depressed in lake water rich in dominant ions, when compared with freshwater lakes with similar nutrient concentrations. In saline lakes with a ratio of TN to TP greater than 12, we tested whether any of these parameters could be correlated with the depressed Chl *a* levels. Due to the small sample size, a multiple regression, with spring TP or summer TP and the parameters listed in Table 4 on summer Chl *a*, was not possible (Sokal and Rohlf 1981, p. 661). Therefore, we calculated predicted summer Chl *a* concentrations (micrograms per litre) from the measured spring TP concentration (micrograms per litre) on the basis of an independent model (Dillon and Rigler 1974) for freshwater lakes:

(2) Predicted log [Chl *a*]
$$= -1.136 + 1.448 \log (\text{observed spring [TP]}).$$

The deviation (D) of predicted log Chl *a* levels (Eq. 2) from the measured log Chl *a* levels,

(3) D = predicted log [Chl *a*] − log (observed [Chl *a*]),

were compared with the variables listed in Table 4. Three conditions were considered prior to analyses of D: (1) Dillon and Rigler's model is valid only for lakes with a TN to TP ratio greater than 12. Thus, D was calculated only for the nine lakes with spring TP data, similar ionic composition, and a TN to TP

TABLE 4. Significant relationships between chemical characteristics and mean summer Chl *a* in 18 lakes in Alberta, excluding both basins of Mink Lake. All correlations are negative except for calcium.

Variable	r^2	P
Conductivity	0.35	<0.02
pH	0.43	<0.01
Sodium	0.36	<0.01
Calcium	0.37	<0.01
Magnesium	0.30	<0.02
Sulfate	0.26	<0.03
Bicarbonate	0.28	<0.03
Carbonate	0.40	<0.01

TABLE 5. Significant relationships (all positive) between chemical parameters and residuals from the phosphorus–chlorophyll model for nine saline lakes (excluding both basins of Mink Lake) in Alberta where the TN to TP ratios are greater than 12.

Variable	r^2	P
TDS	0.78	<0.002
Conductivity	0.78	<0.002
Sodium	0.82	<0.001
Carbonate	0.56	<0.02

ratio greater than 12. (2) Dillon and Rigler's empirical model is valid only for TP levels within the range of their data set. The range of spring TP values in the nine saline lakes used in Eq. 2 is from 46 to 337 $\mu g \cdot L^{-1}$, whereas the range in Dillon and Rigler's data set is from 3 to 180 $\mu g \cdot L^{-1}$. Since a logarithmic transformation is applied, the difference between the values at the upper end of the range (i.e. 180 and 337 $\mu g \cdot L^{-1}$ become 2.26 and 2.53) is small. (3) The deviations D should only be compared with variables that are not correlated with spring TP values, to avoid spurious correlations. The parameters compared with D (conductivity, TDS, Na^+, and CO_3^{2-}) were not correlated with spring TP ($P > 0.25$).

Significant correlations were found between D and TDS, conductivity, Na^+, and CO_3^{2-} (Table 5). The first three correlations were highly significant, e.g.:

$$(4) \quad D = -5.147 + 1.724 \log \text{conductivity} \qquad (n = 9,\ r^2 = 0.78,\ P < 0.002)$$

where conductivity is measured in microsiemens per centimetre. Therefore, in saline lakes with a ratio of TN to TP greater than 12, conductivity, TDS, or Na^+ levels can be used to estimate the deviation of the measured log Chl a levels from values predicted by models developed for freshwater lakes.

The two basins of Mink Lake have been excluded from all regression analyses. Inclusion of Mink Lake data does not change the patterns described for the other 10 saline lakes with a TN to TP ratio greater than 12, with one minor exception. When Mink north and south were included in the regression of summer Chl a on spring TP, the relationship was significant ($n = 11$, $r^2 = 0.55$, $P < 0.01$). However, this regression line is significantly lower than Dillon and Rigler's (1974) freshwater model (similar slopes, $P > 0.1$; different intercepts, $P < 0.001$).

Discussion

The ionic composition of a saline lake influences its productivity. For example, high concentrations of Ca^{2+} can offset the inhibitory effect of high Mg^{2+} concentrations (Vollenweider 1950; Frank 1962; Wetzel and McGregor 1968). Since $CaCO_3$ precipitates at the conductivities present in the study lakes (Gorham et al. 1983), the relatively low Ca^{2+} levels may not offset the toxic effect of high Mg^{2+} concentrations. In addition, the Mg^{2+} values tend to be highest in the more saline lakes, where $CaCO_3$ precipitation would be greatest. The Mg^{2+} toxicity at relatively low Ca^{2+} values could be linked to the positive relationship between Ca^{2+} and summer Chl a and the negative relationships between summer Chl a and the variables in Table 4.

In freshwater lakes, a combination of summer TN and summer TP can explain more of the variation in summer Chl a than can TP alone (Smith 1982). However, spring and summer TN were not significantly correlated with the deviations (D) calculated with Eq. 3 ($P > 0.14$ and 0.69, respectively). The ratio of TN to TP varied from 0.5 to 68 in the study lakes. Only 6 of 20 lakes had a ratio of TN to TP greater than 35, the critical level in Smith's (1982) model. Thus, Smith's model was used to evaluate whether a combination of TN and TP would predict the Chl a levels in the saline lakes better than TP alone. However, as in the previous tests of the saline lake data based on a model developed for freshwater lakes that used only TP, a combination of TP and TN in Smith's model overestimated the Chl a levels in all the study lakes. To illustrate the patterns, the study lakes were divided into three categories based on TN to TP ratios: (1) less than 12, (2) between 12 and 35, and (3) greater than 35. These divisions reflect critical levels in Dillon and Rigler's (1974) and Smith's (1982) models. The measured log Chl a values for each of these categories were compared with the predicted log Chl a values, when the TN to TP ratios were 0.1, 12, and 35 respectively, i.e. the lowest ratio of TN to TP encountered in each of the three categories. Thus, this comparison underestimates the deviation of the predicted from the observed log Chl a values. In all three categories, predicted log Chl a levels for the study lakes were too high (Fig. 3). Thus, regardless of the TN to TP ratio, the relationship between TP, TN, and Chl a is very different in inland saline lakes from that in freshwater lakes.

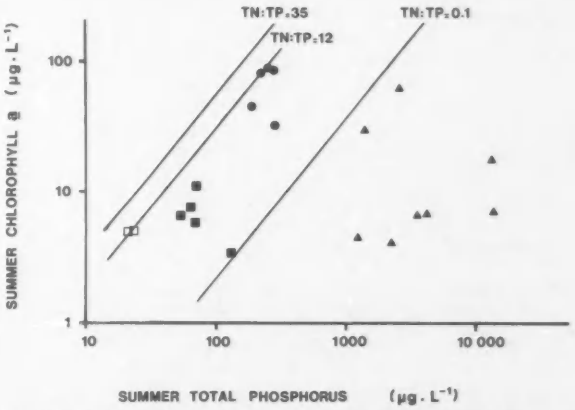

FIG. 3. Relationship between summer TP and Chl a ($\mu g \cdot L^{-1}$) for 20 saline lakes in central Alberta. The diagonal lines are three predictions of Smith's empirical model with different TN to TP ratios (1982). These predictive lines overestimate Chl a levels in each TN to TP category of the saline lakes. Symbol designations are as in Fig. 1.

In our study, no significant correlations were found between any measured form of nitrogen, phosphorus, and summer Chl a in the eight lakes with a ratio of TN to TP less than 12. In the saline lakes with a ratio of TN to TP greater than 12, there was a significant correlation between summer TP and summer Chl a levels, but the ratios of Chl a to TP were consistently lower than in freshwater lakes. In saline lakes with a ratio of TN to TP greater than 12, the deviations between measured and predicted log Chl a levels (from Dillon and Rigler's 1974 model) were highly correlated with conductivity (Eq. 4), TDS, and Na^+. To evaluate further the possible inhibitory effect of salinity on productivity, data are needed on a larger number of temperate saline lakes and experimental work is needed.

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Patterns of Interannual Variation in Age at Maturity of Sockeye Salmon (*Oncorhynchus nerka*) in Alaska and British Columbia

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Peterman, R. M. 1985. Patterns of interannual variation in age at maturity of sockeye salmon (*Oncorhynchus nerka*) in Alaska and British Columbia. Can. J. Fish. Aquat. Sci. 42: 1595–1607.

Interannual variations in mean age of maturity tend to be positively correlated among 10 stocks of sockeye salmon (*Oncorhynchus nerka*) which spawn in rivers emptying into Bristol Bay, Alaska. Taking a comparative approach, I utilized data from British Columbia and Alaska sockeye stocks with different life histories to test alternative hypotheses about sources of these variations in mean age at maturity. The hypotheses included freshwater environment, marine environment, and parental influences. Freshwater hypotheses were rejected and while some parental effects do exist, they are small compared with the effect of events in early marine life. Early marine growth rate data do not exist for these stocks but evidence from five other sockeye stocks shows that fast growth during this period tends to lead to earlier age at maturity.

Les variations d'une année à l'autre de l'âge moyen à la maturité entre 10 stocks de saumon sockeye (*Oncorhynchus nerka*) frayant dans les rivières qui se déversent dans la baie Bristol (Alaska) ont tendance à présenter une corrélation positive. En adoptant une approche comparative, l'auteur a utilisé les données provenant des stocks de saumon sockeye de la Colombie-Britannique et de l'Alaska pour vérifier d'autres hypothèses concernant les sources de ces variations. Les hypothèses mettaient en cause le milieu dulçaquicole, le milieu marin et les influences parentales. Les hypothèses relatives à l'eau douce ont été rejetées et, bien qu'il existe certaines influences parentales, elles sont peu importantes comparativement à l'effet des événements qui se produisent au cours des premiers stades de la vie en mer. En ce qui concerne ces stocks, il n'existe pas de données sur le rythme de croissance aux premiers stades de la vie en mer, mais des indications fournies par cinq autres stocks de saumon sockeye montrent qu'une croissance rapide au cours de cette période a tendance à aboutir à la maturité à un âge plus précoce.

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Numerous theories exist that predict the age at maturity in fishes. These theories are used to explain differences across species (e.g. Schaffer 1974, 1979; Alm 1959; Roff 1982; Stearns 1980) or across populations of the same species (e.g. Schaffer and Elson 1975; Power 1981; Scarnecchia 1983; Jonsson et al. 1984). Variables that affect these predictions include fecundity, survival and growth rates, body size, physiological constraints on early development of eggs, temperature, and, specifically for anadromous salmon, river length and discharge.

These theories have made important contributions to understanding the *average* characteristics of maturity observed in given populations or species. However, factors that cause *variability* across years in mean age at maturity of fish are also of considerable importance to both population biologists and fisheries managers. It is well known that age at first reproduction is one of the most significant parameters in determining rates of change in populations (Cole 1954). Therefore, in order to comprehend and predict population changes, sources of variation in age of first maturity must be understood. Managers of Pacific salmon (*Oncorhynchus* spp.) fisheries are in addition concerned with the effect that changes in mean age at maturity have on the biomass of the catch because (1) Pacific salmon die after reproducing and (2) chum and sockeye salmon (*Oncorhynchus keta* and *O. nerka*) usually become available for harvest only at the time they mature and return toward freshwater. Younger age at maturity in these species would lead to a significant decrease in average weight per fish at maturity for the year class (e.g. Hager and Noble 1976). Unless increased survival rates and growth rates to the earlier ages combine to make up for the decreased average age of fish, total weight of catch may also decrease. There is evidence from Pacific salmon (Bilton 1980; Foerster 1968), walleye (*Stizostedion vitreum*, Spangler et al. 1977), and several clupeoid stocks (Murphy 1977) that growth rates frequently increase at the same time that age at maturity decreases. However, results in Bilton et al. (1982) show for coho salmon (*O. kisutch*) that the total biomass of maturing fish is actually a complex function of several variables, and any factor that causes a decrease in mean age at maturity will decrease total mature biomass under most conditions.

The theories to explain year-to-year variation in mean age at maturity within a species fall into two broad categories, environmental or parental influences. Environmental processes include those factors which affect growth rates and survival rates in both fresh and salt water. For example, Bilton (1980), Bilton et al. (1982), Hager and Noble (1976), and Peterman (1982a) found that smolt size is inversely related to mean age at maturity in coho and sockeye salmon. Ricker (1972) and Godfrey (1958) concluded that hereditary factors also influence age at maturity in salmon. The relative importance of environmental and genetic sources of variation in salmon is still uncertain.

I previously examined one environmental hypothesis by testing whether mean age at maturity in sockeye salmon was density dependent (Peterman 1984a, 1984b). Results showed that mean age at maturity of several Alaska and British

Columbia sockeye stocks was rarely significantly affected by the abundance of sockeye in the Gulf of Alaska, and when it was, some cases showed a positive effect and others a negative one. This lack of significant results prompted the current investigation into what processes might be causing annual variation in mean age at maturity of sockeye stocks. I took a comparative life history approach in which variations in age at maturity were compared for different stocks, some of which shared environments during various segments of their life. These "natural experiments" enable me to test several hypotheses and to identify the early marine life stage as the major source of variation in mean age at maturity.

Methods

Data Sources

In the Gilbert–Rich notation, age 4_2 indicates that a sockeye salmon is in its 4th yr of life since hatching, and that it entered the ocean during its 2nd yr as indicated by the subscript 2 (hence called a sub-2 fish), after rearing one winter as a fry in freshwater (also denoted age 1.2, Foerster 1968, p. 11). Similarly, sub-3 fish are those that smolted after spending two winters in freshwater. In this paper, the total age of fish (say, the 4 in 4_2) is the year of life in which fish mature. In addition, the term "within-sub" refers to comparisons of stocks which all have the same smolt type, such as all sub-2s. "Across-subs" refers to comparisons between sub-2 and sub-3 stocks. Because of lack of data on the sub-3s, all of the British Columbia sockeye stocks used in this analysis are sub-2 fish but the Bristol Bay, Alaska, stocks have extensive data on both sub-2 and sub-3 fish. Most British Columbia and Bristol Bay sockeye salmon reside in the ocean between 2 and 3.25 yr; ages 4_2 and 5_3 exemplify the former and ages 5_2 and 6_3 the latter. Relatively small numbers of sockeye reside in salt water for periods outside that range.

Note that because age at smolting can be identified from adult scales, it is possible to attribute all maturing adults to one smolt type, either sub-2 or sub-3. It is therefore possible to calculate mean age at maturity separately for sub-2 and sub-3 fish, using catch and escapement data by age.

The Bristol Bay sockeye salmon catch and escapement data are available by river systems or fishing district, and by age. Stocks included are those of the Branch, Egegik, Igushik, Kvichak, Naknek, Nuyakuk, Snake, Togiak, Ugashik, and Wood rivers. Catch and escapement data by age cover return years 1956–80; these data are identical to those in Yuen et al. (1981), except they include estimated Japanese high seas catches of maturing fish (provided by C. P. Meacham, Alaska Department of Fish and Game, Anchorage, AK, pers. comm.), as allocated to each stock and age in proportion to the relative total returns to each river system by age. Yuen et al. (1981) also reported total returns by sex. The major age groups 4_2, 5_2, 5_3, and 6_3 comprise an average of 97.8% of Bristol Bay sockeye returns. Rearing lakes for the 10 different Bristol Bay sockeye stocks are separated by up to 300 km. For further details on sources of the Bristol Bay data, see Peterman and Wong (1984). Mean annual smolt lengths were provided for several Bristol Bay stocks, broken down by smolt type, by C. P. Meacham (pers. comm.).

Five British Columbia stocks were used: Babine Lake sockeye and four Fraser River stocks, Adams River, Chilko Lake, Cultus Lake, and Stellako River. Data on total returns (catch plus escapement) for the latter four stocks were provided by the International Pacific Salmon Fisheries Commission (IPSFC) (J. Roos and J. Woodey, pers. comm.). Data were broken down by sub-2 and sub-3 smolt types, but because of the extremely low frequency of the latter (<2%), all analyses of Fraser River fish here were done with sub-2 data only. Babine Lake sockeye return data were from Ricker and Smith (1975), and Department of Fisheries and Oceans (DFO) files (R. Kadowaki, DFO, Prince Rupert, B.C. and C. West, DFO, Vancouver, B.C., pers. comm.). These Babine stock returns included commercial and Indian catch data, by age, as well as escapements. Age structures were estimated from catch sampling programs and samples taken at the Babine Lake counting fence (R. Kadowaki, pers. comm.; also see Peterman and Wong 1984). Only sub-2 data were used for Babine Lake sockeye salmon. For the British Columbia stocks discussed here, over 98% of the fish mature at age 3_2, 4_2, or 5_2. Sex-specific returns data were not available for British Columbia stocks. Rearing lakes for the British Columbia sockeye stocks are separated by as much as 650 km.

Analysis

Mean age at maturity was determined for each brood class separately by smolt type (sub-2 or sub-3) and by sex when data permitted. For a given brood class (offspring of a given year's spawning), the mean age at maturity was calculated as the weighted average total age at which offspring from that brood class, smolt type, and sex returned and were enumerated in the catch and escapement. For example, using the sum of catches and escapements, if the sub-2 population which was spawned in 1970 matured as 3×10^6 age 4_2 and 1×10^6 age 5_2 fish, then the mean age at maturity for the 1970 brood was 4.25 yr. These mean ages at maturity, by brood class, were calculated for 5 sub-2 sockeye stocks in British Columbia, 10 sub-2 Bristol Bay stocks, and 10 sub-3 Bristol Bay stocks. Because male and female returns data were available for the Bristol Bay stocks, mean ages at maturity were calculated separately by sex for those stocks. This detail was felt important because male sockeye frequently mature as jacks but females do not. Jacks are fish that mature after spending only about 1 yr in the ocean; in Bristol Bay, most jacks mature at ages 3_2 or 4_3. Because males have this greater flexibility in their maturation schedule, their age of maturity might tend to vary differently from that of females.

The resulting time series data for mean age at maturity covered from 5 to 28 yr, with most stocks having 12–16 yr of data (Table 1). Linear time trends were fit by ordinary regression, and residuals were calculated by difference from the regression lines. Because there were significant time trends for some stocks at the $\alpha = 0.05$ level, the time trend residuals of all stocks were used in the correlation analyses. For simplicity, the "time trend residual" wording is frequently omitted below, but readers should equate "age at maturity" with time trend residuals thereof.

I correlated the 5- to 28-yr sets of time trend residuals in mean age at maturity of each pair of sockeye salmon stocks first by brood year and then by ocean entry year. In other words, data points were first arranged so that the stocks shared the same brood year (Fig. 1 and example in Fig. 3), and were next arranged so that stocks shared the same calendar year of smolt seaward migration (Fig. 2). This latter pairing of data points by ocean entry year correlated mean age at maturity residuals of sub-2 fish which entered the ocean in year t with the residuals of sub-3 fish which also entered the ocean in year t. Thus, the

TABLE 1. Statistics of weighted mean age at maturity. Sub-2 or sub-3 refers to the populations in which smolts go to sea in their 2nd or 3rd yr of life, respectively, n is the number of brood years with complete data, r is correlation between age at maturity and time, and an asterisk indicates significant correlation with time ($P < 0.05$); historical means and ranges of total age at maturity are also shown.

	sub-2				sub-3			
Stock	n	r	Mean	Range	n	r	Mean	Range
British Columbia								
Adams R.	27	−0.001	4.0	3.8–4.9	—	—	—	—
Babine L.	15	−0.43	4.4	4.1–4.7	—	—	—	—
Chilko L.	27	−0.36	4.1	3.9–4.4	—	—	—	—
Cultus L.	28	−0.40*	4.0	3.8–4.3	—	—	—	—
Stellako R.	28	−0.27	4.1	4.0–4.2	—	—	—	—
Bristol Bay, Alaska								
Branch	12	−0.09	4.5	4.1–4.9	12	−0.12	5.3	4.9–5.9
Egegik	20	−0.01	4.7	4.4–4.9	20	−0.07	5.4	5.1–5.7
Igushik	13	0.07	4.7	4.5–5.0	13	0.05	5.5	5.2–6.0
Kvichak	16	−0.05	4.4	4.0–4.7	16	−0.24	5.2	5.0–5.6
Naknek	15	0.18	4.6	4.3–4.9	15	0.17	5.5	5.1–5.8
Nuyakuk	13	0.42	4.9	4.7–5.0	13	0.17	5.5	5.1–5.9
Snake	5	0.41	4.4	4.1–4.9	5	0.26	5.4	5.1–5.9
Togiak	12	0.73*	4.7	4.4–4.9	12	0.30	5.5	5.1–5.7
Ugashik	19	−0.14	4.5	4.2–4.8	19	0.05	5.2	5.0–5.4
Wood	15	0.10	4.5	4.2–4.9	15	0.19	5.3	5.0–5.8

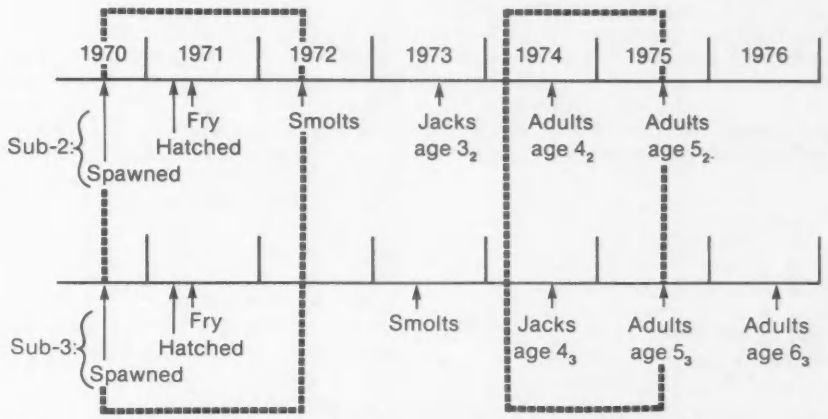

FIG. 1. Example life phase sequences of two life history types of sockeye salmon which were spawned in the same year (same brood year). Top, sequence for a stock in which juveniles migrate to the ocean during their 2nd yr (sub-2s); bottom, sequence for fish which migrate seaward in their 3rd (sub-3s). Broken boxes enclose approximate times when these sub-2 and sub-3 fish are in the same environments.

sub-2 fish were from brood year $t - 2$ and the sub-3 fish were from brood year $t - 3$ (Fig. 2). When correlations were done within smolt types (i.e. one sub-2 stock with another sub-2 stock or one sub-3 stock with another sub-3), it was not necessary to repeat the calculations for both types of lineups of the data (by brood year and by ocean entry year); correlations would be identical because within a smolt type, offspring of the same brood years have identical ocean entry years. This is not true of the correlations between sub-2 and sub-3 data from the same brood year (Fig. 1). The level of significance for the correlations was $\alpha = 0.05$. I examined scatter plots for all correlations to ensure that relations were not nonlinear and that single extreme points were not the cause of significant correlations.

British Columbia sockeye data were not available annually by sex, so the mean age at maturity for those stocks was combined across sexes. To facilitate comparison of British Columbia stocks with Bristol Bay, I also calculated a sexes-combined mean age at maturity for the latter stocks by pooling male and female abundances in the original catch and escapement data.

Within each category of hypothesis tests discussed below, all possible correlations between pairs of stocks were done to test if there was any tendency for covariation among time trend residuals in mean age at maturity. Given the large number of tests of the null hypothesis (H_0) of $r = 0$, about 1 out of 20 tests are expected to be significant at the 0.05 level by chance alone, even if the variates were truly independent. Therefore, I show for each group of tests the probability of getting the observed number of rejections of the null hypothesis by chance alone, as

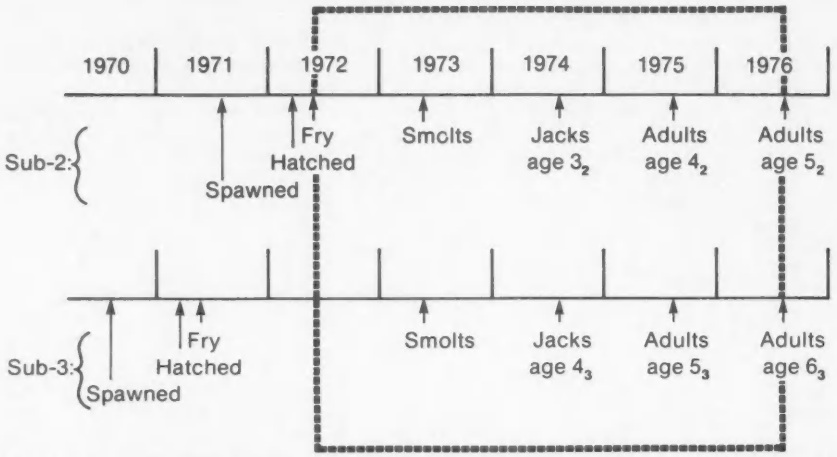

FIG. 2. Example life phase sequences of two life history types of sockeye salmon which enter the ocean in the same calendar year, but which were spawned 1 yr apart. Top, sequence for sub-2s; bottom, sequence for sub-3s. Broken box encloses approximate period in which these sub-2 and sub-3 fish occupy the same environments.

determined from the binomial distribution (individual terms section of National Bureau of Standards 1952; Parsons 1974). Additional information was gained from these large numbers of correlations by examining the signs of the correlation coefficients, a method used by Ricker (1982). Using Chi-square tests with Yates' correction, signs tests were done on each group of correlation coefficients, regardless of the level of significance, to test the null hypothesis that positive and negative correlations appear with equal frequency. By group I mean the set of correlations done within a particular sex and smolt category.

Hypotheses

The environmental and parental hypotheses to explain interannual variations in mean age at maturity within a stock can be broken down into various subsidiary working hypotheses. Environmental sources of variation could arise at any time in the total life span: in early or late freshwater life, in early or late marine life, or a combination thereof. Plausible environmental sources of variation include factors such as temperature, food supply, and disease or predation which might alter the age at which a cohort of fish matures by affecting growth and survival rate. Hypotheses regarding parental influence assume that the age composition of parents affects the mean age at maturity of their offspring through genetic and/or maternal effects. Parental age composition was quantified in three ways: weighted parental total age, smolt age, or ocean age (number of years spent in salt water). For reference, these hypotheses are numbered as follows:

1. Environmental
   a. Total life span or some unspecified portion thereof
   b. Early freshwater life
   c. Late freshwater life
   d. Early marine life
   e. Late marine life
2. Parental
   a. Parental total age composition
   b. Parental smolt age composition
   c. Parental ocean age composition
3. Combination of hypotheses 1 and 2

More specific definitions of the portions of the life span covered by the various environmental hypotheses are as follows (see Fig. 1): 1a. Entire life span or some portion thereof; 1b. Early freshwater life — from the time of egg deposition in year t up to outmigration of the sub-2 smolts in year $t + 2$; 1c. Late freshwater life — from the time of sub-2 smolt outmigration to outmigration 1 yr later of sub-3 fish from the same brood; 1d. Early marine life — from sub-2 smolt outmigration in year $t + 2$ to late winter or early spring of year $t + 4$ when sub-3 fish from the same brood year reach Gulf of Alaska waters occupied by their sub-2 siblings. Late winter or early spring is the time when several studies suggest that these fish reach these waters (French et al. 1976; French and Bakkala 1974, their fig. 4; Hartt 1980); 1e. Late marine life — period from late winter of year $t + 4$ as just described to return of age 5_2 adults in year $t + 5$. Each of these hypotheses assumes that the effect is strong enough to generate a detectable response in age at maturity, despite random variation during the intervening period.

Results

Only two stocks showed significant linear time trends in mean age at maturity, Cultus Lake sockeye and Togiak River sockeye (Table 1). These significant trends meant that the remaining analyses needed to be done with residuals from the time trends. Thus, I was concerned mostly with interannual *variations* around the expected mean age at maturity. Table 1 also gives for each stock the grand mean age at maturity as well as the historical range in mean ages.

Hypothesis 1a — Environmental (Total Life Span)

If the major source of variation in mean age at maturity is some environmental factor, then those fish which share the same environment throughout their lives should tend to have their time trend residuals in mean age at maturity highly positively correlated. Ideally, we should look for such correlations among offspring of different parents which spawn within the same stock in a given year. Such fish are most likely to share the same spatial and temporal environment throughout their lives. How-

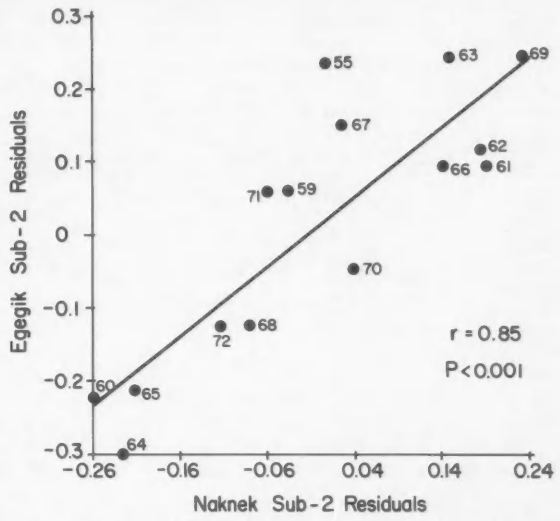

FIG. 3. Example correlation between time trend residuals in mean age at maturity of two different Bristol Bay sockeye stocks (by brood year noted beside data points).

ever, extensive data are not available for wild populations on age of individual sets of parents and their specific offspring, so the best that can be done in the present analysis is to compare fish of different, nearby stocks which are spawned in the same year and which also enter salt water in identical years. Such comparisons across stocks will make it less likely to find statistically significant positive correlations than if fish from the same rearing lakes were used.

Results — Bristol Bay stocks

When data are lined up by brood year, time trend residuals in mean age at maturity tend to be positively correlated (example in Fig. 3). Sub-2 Bristol Bay sockeye males show 11 significant correlations out of 45 correlations performed, and all 11 have positive r values (row 1, Table 2). The probability of obtaining 11 significant correlations out of 45 by chance alone if the ages at maturity of different stocks were independent is <0.001. Therefore, it is very unlikely that these ages are independent. Sub-2 females and sub-3 males show similar results (rows 1 and 2, Table 2), and while sub-3 females do not show a significant number of significant correlations, all four significant cases are positive. In addition, results of signs tests on all the correlation coefficients, regardless of level of significance (rows 1 and 2, Table 3), are consistent with the results in Table 2. Each category of within-sub comparisons by sex in rows 1 and 2 of Table 3 shows a significant predominance of positive correlations. Thus, mean age at maturity tends to vary in the same direction in different Bristol Bay stocks which are spawned and which go to sea in the same years. Hypothesis 1a therefore cannot be rejected.

Results — British Columbia stocks

None of the 10 correlations among British Columbia mean ages at maturity are significant, and in contrast with the Bristol Bay case, only 4 out of the 10 correlations are positive. One aspect of the British Columbia mean age at maturity data could explain the discrepancy with the Bristol Bay results. Four of the five British Columbia stocks are Fraser River fish which consist of over 90% age 4_2 fish, which gives a very small range of variability in age at maturity. This leads to a low power of test, making it less likely to reject the null hypothesis. Because all five British Columbia sockeye stocks examined here are sub-2 fish, analyses by brood year and ocean entry year are identical.

While British Columbia stocks do not show any pattern in mean age at maturity, the frequency of positive correlations in the Bristol Bay data is significantly higher than expected by chance alone. This result justifies a further examination of environmental hypotheses dealing with specific segments of the life of those fish.

Hypotheses 1b and 1e — Early Freshwater and Late Marine Life

Figure 1 illustrates that fish from the same brood year which go to sea in different years (as sub-2 and sub-3 smolts) tem-

TABLE 2. Summary of correlations between mean age at maturity time trend residuals for different Bristol Bay sockeye salmon stocks. Second column shows the type of comparison: whether among sub-2 stocks only, among sub-3s only, or among sub-2 comparisons with sub-3s. The third and fourth columns show the number of significant ($P < 0.05$) correlations and the total number of correlations done in that category, respectively. P, from the binomial distribution, gives the probability of obtaining that many significant cases out of the total number of correlations calculated (an asterisk denotes that there are more significant correlations than expected by chance alone; a dagger denotes fewer than expected). The next column is the number of significant correlations with a positive sign. First three rows are for lineups of data by brood year, and fourth row is by year of smolt entry into the ocean. The Snake River stock had such a short time series of data that one correlation could not be calculated when the brood year lineup was used; hence, only 99 tests exist there.

		Males				Females			
Row	Type of comparison	Signif. tests	Total tests	P	No. of + signif. r	Signif. tests	Total tests	P	No. of + signif. r
				By brood year					
1	sub-2 × sub-2	11	45	<0.001*	11	7	45	<0.01*	7
2	sub-3 × sub-3	10	45	<0.001*	10	4	45	>0.1	4
3	sub-2 × sub-3	1	99	<0.04†	0	6	99	>0.1	2
				By ocean entry year					
4	sub-2 × sub-3	21	100	<0.001*	21	10	100	<0.02*	10

TABLE 3. Summary of signs of all correlation coefficients, regardless of level of significance, calculated between mean age at maturity time trend residuals in different Bristol Bay sockeye salmon stocks. Second column shows the type of comparison. The $+r$/total tests columns show the number of correlation coefficients with positive signs and the total number of correlations done in that category. P gives the probability of obtaining that many positive correlation coefficients out of the total number of correlations calculated, under the null hypothesis that + and − signs are equally likely. An asterisk denotes that there are significantly more + signs than expected by chance alone.

Row	Type of comparison	Males $+r$/total tests	Males P	Females $+r$/total tests	Females P
		By brood year			
1	sub-2 × sub-2	37/45	<0.001*	34/45	<0.005*
2	sub-3 × sub-3	38/45	<0.001*	35/45	<0.001*
3	sub-2 × sub-3	47/99	>0.5	46/99	>0.5
		By ocean entry year			
4	sub-2 × sub-3	86/100	<0.001*	70/100	<0.001*

porally share the early freshwater environment up until the sub-2s enter the ocean. The sub-3s remain in freshwater for an additional year. These sub-2s and sub-3s are also present together in salt water after the sub-3 smolts migrate out to waters occupied by the sub-2 fish (Fig. 1). Therefore, when correlations are calculated between age at maturity of sub-2 and sub-3 stocks which are lined up by brood year, both hypotheses 1b and 1e are tested simultaneously; it is not possible to separate them with this type of analysis. If either or both hypotheses are true, then there should be a strong enough effect to influence age at maturity and there should be a high frequency of significant, positive correlations in age at maturity.

Results — Bristol Bay

Two categories of results exist; the first is for correlations in mean age at maturity across smolt types but *within* stocks, by brood year (i.e. Naknek sub-2s correlated with Naknek sub-3s, Ugashik sub-2s with Ugashik sub-3s, etc.). This is the strongest test of hypotheses 1b and 1e because for most of the 10 Bristol Bay stocks the two smolt types share the same rearing lake in the same calendar year. Another but weaker test is to estimate correlations in age at maturity of sub-2 and sub-3 fish of the same brood year *across* Bristol Bay stocks. This assumes either that those factors which cause variations in mean age at maturity occur during the latter portion of ocean life when fish from these separate stocks have similar space–time distributions, or in early freshwater life. In the latter case it is further assumed that all rearing lakes for these Bristol Bay stocks are equally affected by those weather patterns and subsequent temperature conditions which affect fish growth.

Within-stock correlations between age at maturity of sub-2s and sub-3s show no significant tendency for either positive or negative correlations ($P > 0.8$), and only 1 of 20 correlations is significant (brood year columns in Table 4). Both collections of 99 within- and across-stock comparisons likewise show few significant correlations (row 3, Table 2), and positive and negative signs of the correlation coefficients occur with almost equal frequency (row 3, Table 3).

These results lead to a rejection of both hypotheses 1b and 1e.

TABLE 4. Signs of correlations between time trend residuals in mean age at maturity of sub-2 and sub-3 populations of Bristol Bay sockeye salmon, within stocks. Analyses by brood year and by ocean entry year are separated. An asterisk denotes significant correlation ($P < 0.05$).

Stock	Males By brood year	Males By ocean entry year	Females By brood year	Females By ocean entry year
Branch	−0.30	+0.31	−0.01	+0.01
Egegik	+0.18	+0.28	+0.52*	+0.16
Igushik	−0.32	+0.24	−0.23	+0.16
Kvichak	−0.29	+0.14	−0.08	+0.05
Naknek	+0.32	+0.43	+0.13	+0.51
Nuyakuk	−0.30	+0.46	+0.15	+0.28
Snake	+0.25	+0.97*	+0.97	+0.99*
Togiak	+0.10	+0.75*	+0.33	+0.75*
Ugashik	+0.09	+0.10	−0.24	+0.22
Wood	+0.32	+0.39	−0.11	+0.08

Whatever factors caused the positive correlations in the within-sub comparisons by brood year in the previous section do not occur in either early freshwater or late marine life.

Hypothesis 1e — Late Marine Life

An additional but weaker test of environmental hypothesis 1e, dealing with late marine life, is derived from analyses of British Columbia mean age at maturity data, with sexes combined. The spatial and temporal distributions of British Columbia and Bristol Bay sockeye salmon overlap to some extent in the Gulf of Alaska from about 8–12 mo after smolts enter the ocean until they mature (French et al. 1976; Hartt 1980). If environmental variations during this period of overlap were largely responsible for variations in mean age at maturity, then variations in age at maturity of British Columbia and Bristol Bay sockeye stocks should be positively correlated. For this particular set of correlations only, the sexes-combined mean age at maturity data were used for Bristol Bay stocks.

Results — British Columbia and Bristol Bay

Only 3 out of 50 correlations between age at maturity of British Columbia sub-2 fish and Bristol Bay sub-2 stocks are significant, fewer than expected by chance alone ($P > 0.2$). Only one of these significant r values is positive and when signs of all 50 r values are examined, only 26 out of 50 are positive. The use of age at maturity from data in which sexes were combined does not explain this lack of correlation because the sexes-combined Bristol Bay data show almost identical results to the sexes-separate analysis discussed earlier (12 out of 45 sub-2 × sub-2 correlations significant, all 12 r values positive; cf. row 1, Table 2). This lack of positive correlation between Bristol Bay and British Columbia sockeye ages suggests that late ocean life is not a major source of variation in age at maturity. However, this evidence is relatively weak because Bristol Bay and British Columbia sockeye spatially overlap more during the winter than the summer, when most growth takes place (French et al. 1976). Despite this fact, the hypothesis about late ocean life appears highly improbable because of the analysis in the previous section which relied on comparisons of sub-2 and sub-3 fish of Bristol Bay only.

Hypotheses 1c and 1d — Late Freshwater and Early Marine Life

Sub-2 fish that are spawned in year t go to sea in the same calendar year as sub-3 fish spawned in year $t - 1$ (Fig. 2). They also share the late freshwater environment as well as all of their marine environments (Fig. 2). Thus, when correlations are done between sets of mean age at maturity data using this lineup of data by ocean entry year, I am comparing fish that share the environment for a large segment of their life. Because I rejected the late marine environmental hypothesis (1e) in previous sections, the early marine life segment is the most likely source of saltwater environmental variation in age at maturity. The late freshwater stanza has also not yet been addressed. By using a lineup of data by ocean entry year the two hypotheses dealing with the late freshwater and early marine sources of variation can be examined, but not separately. If either or both hypotheses are valid, then there should be a high frequency of significant, positive correlations between mean age at maturity in different stocks when data are arranged by ocean entry year.

Results — Bristol Bay

As in the previous test for hypotheses 1b and 1e, there are two categories of results: one in which only within-stock comparisons of sub-2s and sub-3s are examined and one in which all Bristol Bay sub-2 stocks are compared with all other Bristol Bay sub-3 stocks. The former test is for fish which are likely to share the same rearing lakes and migration routes in the same years and the latter is for different stocks which only are at the same life stage in the same years from late freshwater onward.

All within-stock correlations between mean age at maturity of sub-2s and sub-3s by ocean entry year are positive (ocean entry year columns in Table 4). The 100 within- and across-stock comparisons of sub-2s and sub-3s similarly show a significantly ($P < 0.02$) large number of significant correlations, all of which are positive for both males and females (row 4, Table 2). As well, the signs of all 100 correlation coefficients, regardless of level of significance, show a significant predominance of + signs (row 4, Table 3).

The marked contrasts in results between the "brood year" and "ocean entry year" columns of Table 4, and between rows 3 and 4 of Tables 2 and 3, clearly show that by lining data up by ocean entry year instead of brood year leads to significant positive covariation in mean age at maturity of most Bristol Bay sockeye stocks. This failure to reject hypotheses 1c and 1d (dealing with late freshwater and early salt water) means that strong environmental sources of variation are most likely to occur somewhere in those two periods, because hypotheses 1b and 1e were rejected above.

Hypothesis 1c — Late Freshwater

A different set of tests can be used to examine the late freshwater hypothesis separately from the early marine life hypothesis. The late freshwater hypothesis assumes that the tendency for variations in mean age at maturity to be positively correlated across all 10 Bristol Bay stocks and across smolt types is due to variations in factors which directly or indirectly affect fish growth in freshwater (e.g. lake temperature, Foerster 1968). Large-scale weather patterns could cause variations in lake temperature to be positively correlated across lakes which are separated by hundreds of kilometres. If this were true, then in order to explain the common pattern of variation in age at maturity in Bristol Bay stocks, at least two conditions must hold. (1) Time trend residuals in annual mean smolt sizes must be positively correlated across stocks when data are lined up by ocean entry year (so that their last year of freshwater growth is identical). This correlation should be true particularly for stocks that showed significant positive correlations in mean age maturity in Table 2. (2) The smolt size residuals must be significantly correlated with mean age at maturity time trend residuals. Both conditions 1 and 2 must hold to accept the late freshwater hypothesis. A third condition is expected if this hypothesis is true. (3) Correlations by ocean entry year between time trend residuals in mean age at maturity of sub-2s of one stock and those of the sub-3s of another should be inversely related to the distance separating their rearing lakes, because distant lakes are less likely to share common variations in temperature than nearby lakes. In other words, under hypothesis 1c, the farther apart rearing lakes are, the less correlated the variations in freshwater factors which affect age at maturity should be. To take into account the effect of different sample sizes on the confidence in r estimates, I use the probability from the hypothesis test $r = 0$, rather than the actual r value. Condition 3 can then be reworded: the probability for H_0:$r = 0$ should increase with increasing distance between rearing lakes. Sub-2 comparisons with sub-3s are necessary here because when using the ocean entry year lineup, the only portion of their freshwater life they share is the last year for the sub-3s (Fig. 2).

Results

This hypothesis is rejected because none of the three conditions holds.

Condition 1 — Time trend residuals in mean smolt size for fish which enter the ocean in the same year do have a tendency to be positively correlated. The strongest cases are, of course, for fish of different smolt types which rear in the same lakes (bottom section Table 5). But because most of the positive correlations between mean age of maturity time trend residuals shown in each category of Table 2 are due to comparisons *across lakes*, the top three sections of Table 5 are most relevant. For those cases in which smolt data exist, it is more revealing to test if both of the following types of correlations are significant: (i) a significant positive correlation between mean age at maturity of two stocks and (ii) a significant positive correlation in the smolt sizes of those same two stocks. Table 5 shows that in the six cases in which smolt sizes are significantly correlated, only one of those cases also has the mean age at maturity significantly correlated (Kvi_2–Nak_3). Similarly, of the four cases in which age at maturity varies together, only one of those also has smolt size of the two stocks significantly correlated. Thus, condition 1 is not supported strongly.

Condition 2 — In only one of six populations was the smolt size time trend residual significantly correlated with time trend residuals in mean age at maturity (Naknek sub-2s, $r = -0.64$, $P = 0.01$). Exactly half of these correlation coefficients were positive. Therefore, condition 2 does not hold.

Condition 3 — Probability values for the correlation among time trend residuals in sub-2 and sub-3 age at maturity are not related to distance between rearing lakes of the respective stocks (males, $r = 0.08$, $P > 0.5$, $n = 100$; females, $r = -0.09$, $P > 0.5$, $n = 100$). These data covered all 10 Bristol Bay stocks discussed here.

The failure of any of the three conditions to hold leads to a rejection of hypothesis 1c, that variation in the late freshwater environment is largely responsible for variations in mean age at maturity.

TABLE 5. Correlations in smolt size time trend residuals across various Bristol Bay sockeye stocks; data are lined up so that fish enter the ocean in the same year. Stock names are abbreviated and smolt types are designated sub-2s or sub-3s. Males and females columns show correlations between mean age at maturity time trend residuals of the pair of stocks indicated at the left. An asterisk denotes significant correlation ($P < 0.05$).

				Age at maturity			
	Smolt weights			Males		Females	
Stocks	r	P	n (yr)	r	P	r	P
Sub-2s, across lakes							
Kvi_2–Nak_2	+0.43	0.09	16	0.74	<0.01*	0.27	0.35
Nak_2–Uga_2	−0.20	0.47	15	0.68	<0.01*	0.60	<0.02*
Uga_2–Kvi_2	+0.36	0.22	13	0.65	<0.01*	0.30	0.24
Sub-3s, across lakes							
Kvi_3–Nak_3	+0.75	<0.001*	17	0.34	0.26	0.20	0.52
Nak_3–Uga_3	−0.11	0.69	15	0.29	0.29	0.36	0.19
Uga_3–Kvi_3	+0.27	0.36	14	−0.17	0.54	−0.46	0.08
Sub-2s × sub-3s, across lakes							
Kvi_2–Nak_3	+0.59	<0.02*	16	0.61	0.02*	0.16	0.59
Kvi_2–Uga_3	+0.23	0.44	13	0.44	0.09	−0.02	0.95
Kvi_3–Nak_2	+0.70	<0.01*	17	0.09	0.78	0.14	0.64
Kvi_3–Uga_2	+0.14	0.62	14	−0.29	0.27	−0.48	0.06
Nak_2–Uga_3	−0.08	0.77	15	0.00	0.99	0.08	0.78
Uga_2–Nak_3	+0.05	0.86	15	0.12	0.67	0.06	0.83
Sub-2s × sub-3s, within lakes							
Kvi_2–Kvi_3	+0.77	<0.001*	15	0.14	0.62	0.05	0.87
Nak_2–Nak_3	+0.72	<0.001*	18	0.43	0.11	0.51	0.05
Uga_2–Uga_3	+0.60	<0.02*	15	0.10	0.69	0.22	0.36

Hypothesis 1d — Early Marine Life

All but two of the environmental hypotheses have been eliminated. The first is hypothesis 1a, which states that at some unspecified point in their life, the age of maturity of sockeye salmon is significantly affected by some environmental factor. The second is hypothesis 1d, which specifies the early marine life as the source of variation. Because this second hypothesis is the more specific case of the first hypothesis, only the second, early marine case will be considered further. A strong test of this hypothesis is to relate variation in early marine growth of fish to variations in mean age at maturity. Data are not available on actual smolt-to-adult growth rates for the Bristol Bay stocks discussed here because back-calculations of sizes of smolts from scales have not been done for these stocks. In fact, accurate back-calculations of smolt sizes may never be feasible for these stocks because of their peculiar scale patterns caused by a lack of significant growth frequently observed during the first few weeks at sea (H. W. Jaenicke, National Marine Fisheries Service, Juneau, AK, pers. comm.).

Results

While data are not available for the Bristol Bay sockeye stocks, five tests of this hypothesis with other sockeye stocks show that early marine growth (calculated from scales) is related to age at maturity. Three cases are for British Columbia stocks, one for an Alaskan stock, and one for an Asian stock. In Babine Lake sockeye, Bilton (1970) examined two periods of ocean growth, from the freshwater annulus to the first ocean annulus, which is formed in January (Bilton and Ludwig 1966), and from the first to the second ocean annulus. Using 6 brood years' data, Bilton (1970) found that growth in the first period did not have any relation to age at maturity but growth during the second period did. The mean width of the scale from the first to second ocean annulus in fish which matured at age 4_2 was significantly greater in all years than in fish which matured as 5_2s. Thus, fish that grew faster during their early marine life matured earlier.

Krogius (1960) showed, by back-calculating fish growth from scales sampled in 8 brood years, that beginning in the first summer at sea, early-maturing sockeye grew much more quickly than late-maturing fish from the same brood. This was true even for cases in which the freshwater growth did not differ significantly between fish which later matured at age 3 or 4.

In Chilko Lake sockeye, data covering 8 brood years show that faster growth during the first 6–8 mo of ocean life is related to earlier mean age at maturity (IPSFC 1962). To my knowledge, no other growth period was examined. Data from subsequent years corroborate these earlier findings, especially when ocean temperature during the 1st yr at sea is taken into account (J. Woodey, IPSFC, New Westminster, B.C., pers. comm.). Foerster (1968, p. 355) also discussed Cultus Lake, B.C., and Karluk Lake, AK, sockeye, which show the same pattern of fast early marine growth leading to early maturation.

If such a relation holds for the Bristol Bay sockeye stocks, then the evidence would tend to further support hypothesis 1d, that environmental conditions during the first months of marine life influence growth during that time, and hence also affect age at maturity. This effect of an environment common to several stocks would explain the tendency for positive correlation in mean age at maturity among populations which have the same ocean entry year.

Hypotheses 2a, 2b, 2c — Parental Age Composition

Age composition of the parents, measured by total, ocean, or smolt age, could be the major determinant of mean age at

TABLE 6. Summary of pairwise correlations between time trend residuals in mean age of spawners in year t of different Bristol Bay sockeye salmon stocks. Second column shows type of age measure used for each stock (see text). Third and fourth columns show the number of significant ($P < 0.05$) correlations out of the total number of correlations done in that category, respectively. P gives the probability of obtaining that many significant cases out of the total number of correlations calculated (an asterisk denotes that there are more significant correlations than expected by chance alone). Next column is the number of significant correlations with a positive sign. The $+r$/total tests column shows the number of correlation coefficients with positive signs (regardless of level of significance) and the total number of correlations done in that category. The last P column gives the probability of obtaining that many positive correlation coefficients out of the total number of correlations calculated, if + and − signs were equally likely (an asterisk denotes significantly more positive correlations than expected).

Row	Age measure	Signif. tests	Total tests	P	No. of + signif. r	$+r$/total tests	P
1	Mean total age, combined across smolt types	18	45	<0.001*	18	42/45	<0.001*
2	Mean ocean age, combined across smolt types	34	45	<0.001*	34	44/45	<0.001*
3	Mean smolt age, combined across smolt types	10	45	<0.001*	10	31/45	<0.02*
4	Mean total (or ocean) age of sub-2s	27	45	<0.001*	27	44/45	<0.001*
5	Mean total (or ocean) age of sub-3s	30	45	<0.001*	30	44/45	<0.001*

maturity of their offspring. As shown previously, there is a significant tendency for variation in total age at maturity to be positively correlated among fish which were spawned in the same brood year and which entered the ocean in identical years (rows 1 and 2, Table 3). In order for any parental hypothesis to be a sufficient explanation of this observation on *within*-sub comparisons, two conditions must hold: (1a) age composition of parents that produce the given smolt-type of offspring must be positively correlated among stocks in given years of spawning, t, and (1b) age composition of offspring of a given stock must be signficantly correlated with age composition of their parents. Two conditions are also necessary to explain the second observation of positive correlations in the *across*-sub comparisons of age at maturity done for fish which enter salt water in the same year (row 4, Table 3): (2a) the age composition *in year t* of spawners that produce *sub-3* offspring must be positively correlated with age composition *in the following year* of spawners that produce *sub-2* offspring (see Fig. 2) and (2b) the same as 1b. The above conditions must hold for at least one measure of age composition.

Data do not exist to permit calculation of the mean age of spawners which actually give rise to the sub-2 offspring. Sub-2s are probably produced by parents with a variety of smolt life histories, and the same is likely for sub-3s. I used two compromise procedures; in one I calculated the mean age composition of all spawners, regardless of their smolt type, and in the other I separated sub-2 and sub-3 spawners. These two methods covered the extremes in the range of possibilities. I refer to the weighted mean age calculated by combining parents of all smolt types as the "combined" mean age and I calculated "combined" mean ages of spawners for each of the three age measures: total, ocean, and smolt age. In contrast, mean age of spawners, separated by smolt type, only includes total age because within a sub-2 or sub-3 category, the mean ocean age is simply total age minus a constant. All correlation analyses using total ages within subs will therefore be identical to the within-sub ocean age cases.

Note that all the above correlation analyses are for time trend residuals in mean age of spawners to make these analyses parallel to the previous ones. This was done even though no significant time trend exists in any spawner age measure for any of the 10 Bristol Bay sockeye stocks (all $n \geq 20$, $P > 0.1$).

Results

Condition 1a — Mean age of spawners in year t is generally positively correlated among Bristol Bay sockeye salmon stocks, no matter which measure of age structure is used (Table 6). There are large numbers of significant correlations in each age category and all significant cases have positive signs. In addition, when all correlation coefficients are examined, regardless of level of significance, most are positive (Table 6). These results are for age of spawners in year t, so condition 1a is met.

Condition 2a — Mean age of spawners in year t is in some cases significantly correlated with the mean age of spawners in year $t + 1$, but there is no consistent pattern (Table 7). When total ages combined across smolt types are used, more significant correlations exist than expected by chance alone ($P < 0.01$), but 5 of the 11 signs are negative. When all 100 r values are examined, no tendency toward + or − signs exist ($P > 0.5$, Table 7). A similar pattern holds for the case in which mean total age of sub-2 spawners in year $t + 1$ is correlated with mean total age of sub-3 spawners in year t (row 4, Table 7). In the cases of ocean age of all spawners and smolt age of all spawners, few significant correlations exist (rows 2 and 3, Table 7). Signs tests show that ocean ages of all spawners combined tend to be negatively correlated in successive spawning years, whereas smolt ages tend to be positively correlated.

This lack of consistent pattern among the significant categories of Table 7 shows that condition 2a is not met and so the parental effect hypothesis cannot be an explanation of the high frequency of positive correlations in the sub-2 × sub-3 comparisons by ocean entry year (row 4, Table 3). However, the consistent patterns in Table 6 do partly explain the high frequency of positive correlations in within-sub comparisons

TABLE 7. Summary of correlations between time trend residuals in mean age of spawners in year of spawning t (X variate) and in year of spawning $t+1$ (Y variate, see text). Second column shows age measures of both X and Y variates. Asterisks defined as in Table 6.

Row	Age measure	Signif. tests	Total tests	P	No. of + signif. r	+ r/total tests	P
1	Mean total age, combined across smolt types	11	100	<0.01*	6	53/100	>0.5
2	Mean ocean age, combined across smolt types	6	100	>0.1	0	39/100	<0.05*
3	Mean smolt age, combined across smolt types	2	100	>0.05	2	69/100	<0.005*
4	Mean total age of sub-2 $(t+1)$ × mean total age of sub-3(t)	10	100	<0.02*	6	43/100	>0.1

TABLE 8. Summary of correlations between time trend residuals in mean age of spawners and time trend residuals in mean age of their offspring, for each of 10 different Bristol Bay sockeye salmon stocks. Asterisks defined as in Table 6.

Row	Age measure	Signif. tests	Total tests	P	No. of + signif. r	+ r/total tests	P
1	Mean total age, combined across smolt types	0	10	>0.5	0	7/10	>0.2
2	Mean ocean age, combined across smolt types	4	10	<0.001*	4	8/10	>0.1
3	Mean smolt age, combined across smolt types	1	10	>0.3	1	10/10	<0.001*
4	Mean total (or ocean) age of sub-2s	0	10	>0.5	0	7/10	>0.2
5	Mean total (or ocean) age of sub-3s	0	10	>0.5	0	6/10	>0.5

(rows 1 and 2, Table 3). Therefore, a test must be made of the condition that age composition of parents and their offspring are significantly correlated.

Condition 1b — In some cases, parent and offspring age compositions are significantly correlated (Table 8). These parent–offspring correlations are again done in two ways because of the uncertainty surrounding the actual parents of the particular smolt types in the offspring. Mean ages of spawners in a given brood year and mean ages of their offspring are first calculated by combining all smolt age groups, and second by smolt type separately. The "combined" ocean age category does show that ocean age of parents (regardless of their smolt type) tends to be positively correlated with ocean age of their offspring (again regardless of their smolt type) (row 2, Table 8). Four of the stocks (more than expected by chance alone) have significant correlations and all are positive. In no other age category is there a significant number of significant correlations, and only in the "combined" smolt category is there a significant trend in the collection of signs (row 3, Table 8).

Because conditions 1a and 1b are met, the parental influence hypothesis cannot be rejected as an explanation of the positive correlations in mean age at maturity for the within-sub comparisons (rows 1 and 2, Table 3). But the failure of condition 2a to hold refutes the parental hypothesis as an explanation of the positive correlation in mean age at maturity among sub-2 and sub-3 broods which entered the ocean in the same year (row 4, Table 3).

Environmental vs. Parental Influences in Bristol Bay Stocks

I estimated the relative importance of environmental versus parental influences on annual variations in age at maturity by comparing mean r values for two different situations: Type A cases in which parental, freshwater, and marine environmental influences are held in common among the stocks, and Type B cases in which only late freshwater and marine environmental effects are shared. Type A cases thus include the additional effect of parental and early freshwater influences, which Type B cases do not. To test whether those parental and early freshwater factors significantly affect age at maturity, I tested the null hypothesis that the mean correlation coefficient for Type A cases, r_A, equals that for Type B cases, r_B. Failure to reject H_0 means that I cannot conclude that parental and early freshwater influences are significant in comparison with environmental effects in the remaining portion of the life.

Type A cases include correlations in time trend residuals of mean age at maturity between pairs of populations with the same smolt age, brood year, and ocean entry year. These 90 correlations for each sex are those summarized previously (rows 1 and 2, Table 2). Type B cases include the 100 correlations between

TABLE 9. Values in the steps in calculating the relative importance of environmental and parental influences on time trend residuals in mean age at maturity. Mean symbols are defined in the text; source indicates how the means were calculated; n = sample size (number of r values used to calculate the mean z values). Last two rows give t statistics and the associated probabilities for $H_0: r_A = r_B$.

Mean	Source	n	Male	Female
z_{A2}	sub-2 × sub-2	45	0.471	0.311
z_{A3}	sub-3 × sub-3	45	0.435	0.224
z_A	$(z_{A2} + z_{A3})/2$	45	0.453	0.268
z_B	sub-2 × sub-3 by OEY	100	0.370	0.206
t			0.45	0.34
P			>0.5	>0.5

pairs of populations with different smolt ages, but with the same ocean entry year (summarized in row 4, Table 2). As shown above, Type A spawner ages tend to be positively correlated across stocks (Table 6), whereas Type B cases are not (Table 7). To calculate the mean correlation coefficient for Type A cases, I converted each of the correlation coefficients, r, to a z value using Fisher's z-transform ($z = 0.5[\log_e(1 + r) - \log_e(1 - r)]$, Kendall and Stuart 1977, p. 419). This avoided the problem that r values are not additive or normally distributed. A mean z was calculated by weighting each z by its sample size (years). Two mean z values resulted, one for sub-2 correlations (z_{A2}) and one for sub-3 cases (z_{A3}). The average of these two means is denoted z_A. The 100 Type B cases were handled similarly, resulting in z_B. I tested $H_0: r_A = r_B$ by doing a t-test on these z_A and z_B values (Sokal and Rohlf 1969, p. 521). These calculations were done separately by sex.

Results

Parental and early freshwater influences on variations in age at maturity are not significant for either sex (Table 9) because Type A and Type B mean correlation coefficients are not significantly different ($P > 0.5$). If parental or early freshwater effects were strong, the Type A mean correlation coefficient should have been significantly larger than the Type B coefficient because only Type A cases share early freshwater life and have positively correlated parental ages (Table 6).

Discussion

Environmental vs. Parental Effects

Variations in mean age at maturity of Bristol Bay sockeye stocks tend to be most positively correlated when stocks enter salt water in the same calendar year. Most of the variations are related to unknown events which occur during the early marine life of these fish; freshwater, late marine, and parental influences appear relatively unimportant.

This importance of the early marine environment is understandable in light of evolutionary and physiological arguments. Plasticity in age at maturity is an adaptation to environmental variation which maximizes fitness by trading off future growth and mortality (Stearns and Crandall 1984). If sockeye had a genetically predetermined schedule for age at maturity, then fitness would be reduced when environmental conditions changed. While the range of mean age of maturity in sockeye is undoubtedly under some genetic constraints (they do not mature at age 2 or age 10), the interannual variability in that age is not expected to be under strong genetic control because of the large variability in the oceanic habitat (Wooster 1983). The early, rather than late, marine environment is critical because evidence from Atlantic salmon (*Salmo salar*) stocks shows that fish start to channel energy into gonads at least 1 yr before they mature (Sutterlin and MacLean 1984).

Other data suggest that while environmental effects in early marine life may shift first age of maturity forward or back in time, the maturity schedule of the remaining brood class is relatively fixed after this life stage. There is a significant positive correlation in most Bristol Bay sockeye stocks between the abundance of maturing sockeye of age n in year t and that of age $n + 1$ in year $t + 1$ (Peterman 1982b). If environmental variations *after* the first age at maturity were important in revising the maturity schedule of the portion of the brood remaining in the ocean, then such correlations would be rare.

The comparative life history approach used here could be improved upon by doing multiple regression of variations in age at maturity on parental age and several environmental variables. However, this approach is not feasible now because we do not know which environmental variables are most appropriate, and very few long data series exist for such variables. The above conclusion concerning the relative importance of environmental and parental influences as determined by the comparative life history approach will probably not change qualitatively even if a better multiple regression approach becomes possible in the future. This conclusion arises from two observations: (1) sub-2 and sub-3 fish which were spawned 1 yr apart and which entered the ocean in the same calendar year do tend to have positive correlations in age at maturity (row 4, Table 2), and (2) the age compositions of parents of those two groups generally are not positively correlated (Table 7). Thus, environmental influences tend to override parental effects.

Parent–offspring correlations in age at maturity reported here do not represent direct measures of heritability (h^2) because actual parents were unknown for particular offspring. Only mean population ages were measurable. However, nonrandom mating and reproductive success with respect to age of spawners (Hanson and Smith 1967) tend to make parent–offspring r values reported here underestimates of the true values. On the other hand, parental effects may be overestimated by current parent–offspring r values because periodic patterns of environmental factors (Mysak et al. 1982) would tend to make variations in offspring age at maturity resemble those of their parents, even if there were no parental effect. For example, if ocean temperature changes to a new value for long enough, it may affect the age at maturity of some spawning populations, as well as the age of their offspring. This would increase the parental–offspring correlation. Parental effects include factors of both genetic and nongenetic (larger females lay larger eggs, which in turn hatch into larger fry, etc.) origin. These factors will be examined in an analysis to be published elsewhere.

Related Research

Few researchers have investigated causes of variation in mean age at maturity of sockeye salmon. In a study of age-structured catch data for sockeye from the Rivers Inlet and Skeena River, B.C., stocks, Godfrey (1958) came to a conclusion opposite mine. He felt that hereditary factors were a much more important determinant of age at maturity than environmental influences. However, Godfrey's analysis was biased by analysis of catch

data only, and by his assumptions that environmental factors vary randomly in time and that only genetic effects generate periodic patterns in abundance of given age classes. Oceanographers have documented several 4- to 6-yr periodic patterns of variation (see Wooster 1983), and Larkin (1971) showed how depensatory predation can cause similar cycles in abundance. Therefore, Godfrey's method probably overestimated the relative importance of genetic effects and underestimated the extent of environmental effects. Ricker (1972) reviewed evidence which showed that both genetic and environmental factors affect age at maturity in sockeye. Other authors mentioned in the section concerning hypothesis 1d (early marine life) did not estimate the relative importance of parental and environmental effects on age at maturity of sockeye, but they did show that faster early marine growth leads to earlier maturation in sockeye.

Age at maturity has also been investigated in other Pacific salmon species. Helle's (1979) results for Alaskan chum salmon were similar to Bilton's (1970) for Babine Lake sockeye. Helle showed that mean age at maturity is inversely related to growth rate between the first and second winter at sea, but is uncorrelated with growth between date of ocean entry and the first winter (when the first ocean annulus is formed on scales). Hager and Noble (1976), Bilton et al. (1982), and many other authors, working on chinook (*O. tshawytscha*) and coho salmon documented the effect of larger size of release of artificially reared fish on age at maturity. These experiments have generally moved average body size of seaward migrating fish outside the range observed in wild populations, and it is therefore not surprising that the importance of freshwater growth was increased. In addition, breeding experiments with chinook salmon showed age at maturity to be heritable, with males and females affected differently (reviewed in Ricker 1972, p. 79).

Results here for sockeye salmon are also similar to those for other species groups in which environmental factors are known to affect age at maturity (e.g. Ritter 1975; Saunders et al. 1983; Alm 1959).

Research and Management Implications

Because sockeye salmon differ considerably in weight at different ages, variations in mean age at maturity can have profound effects on total weight of the catch from a brood class and fecundity of the spawning stock. Some fishing gear used on sockeye salmon (e.g. gill nets) is selective and results in higher survival of small "jacks" than of adults (Ricker 1982). Results here showing a lack of significant parental effects suggest that this selectivity may be relatively unimportant in changing the maturity schedule. However, before recommending that managers ignore this facet of gear selection, my conclusions should be tested by controlled sockeye breeding experiments using offspring of known parents reared in various oceanic environments. Experiments similar to this have been done on Atlantic salmon (Naevdal 1983; Saunders et al. 1983).

Finally, management agencies are attempting to artificially manipulate sockeye abundance through lake fertilization and spawning channels. If large increases in high seas abundance of sockeye are ever achieved, they could alter the growth environment to the point where mean age at maturity is increased, along with mortality. While density-dependent marine growth has been documented for sockeye, density-dependent survival or age at maturity has not occurred over the historical range of abundance (Peterman 1984b). The rising long-range expectations for future sockeye enhancement programs in the North Pacific should cause us to put high priority on the experiments mentioned above on sources of variation in age at maturity.

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Effects of Abundance and Water Temperature on Recruitment and Growth of Alewife (*Alosa pseudoharengus*) near South Bay, Lake Huron, 1954–82[1]

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Henderson, B. A., and E. H. Brown, Jr. 1985. Effects of abundance and water temperature on recruitment and growth of alewife (*Alosa pseudoharengus*) in South Bay, Lake Huron, 1954–82. Can. J. Fish. Aquat. Sci. 42: 1608–1613.

Analysis of catches in pound nets provided indices of population size (ages 2–6) and of recruitment (ages 4–6) for alewives (*Alosa pseudoharengus*) spawning in South Bay (1954–82). Four hypotheses concerning the effects of stock size and water temperature on growth and recruitment were tested statistically. The number of recruits per spawner was not a function of parental stock size, but was dependent on surface-water temperatures in June and July. Although the size of both males and females at age 3 yr was positively related to surface-water temperatures in the three preceding summers, growth rates were only a function of water temperatures during the second year of growth (age 1). However, growth rates during the first, second, and third years of growth were all related to year-class strength. Thus, population abundance, through recruitment, was determined by an abiotic factor (water temperature), but growth was mostly affected by intraspecific competition for, presumably, food.

L'analyse des prises à l'aide de trappes fixes a fourni des indices du nombre (de 2 à 6 ans) et du recrutement (de 4 à 6 ans) chez le gaspareau (*Alosa pseudoharengus*) qui fraie dans la baie South (1954–1982). Des analyses statistiques ont servi à la vérification de quatre hypothèses sur les effets de la taille du stock et de la température de l'eau sur la croissance et le recrutement. Le nombre de recrues par géniteur dépendait des températures superficielles de l'eau en juin et juillet, mais n'était pas fonction de la taille du stock parental. Quoique la taille des mâles et des femelles de 3 ans était en relation positive avec les températures superficielles de l'eau au cours des trois étés précédents, les taux de croissance n'étaient fonction des températures de l'eau qu'au cours de la deuxième année de croissance (1 an). Toutefois, les taux de croissance au cours des première, deuxième et troisième années de croissance étaient liés à la fréquence numérique de la classe d'âge. Ainsi, la taille de la population par recrutement était déterminée par un facteur abiotique (température de l'eau), mais la croissance était principalement touchée par la compétition intraspécifique pour la nourriture, en théorie.

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The marine alewife (*Alosa pseudoharengus*) was first recorded in Lake Huron in 1933 (MacKay 1934) and since then has become an important member of the fish community (Smith 1970). The purpose of this study was to determine whether the abundance and growth of alewife sampled in South Bay (Fig. 1) were influenced by stock size (Brown 1972) and water temperature (Colby 1973). These questions were considered to be particulary relevant to an exotic species colonizing a lake in the absence of naturally evolved control (Elton 1966). Undeniably, abundance and water temperature are only two of the factors that might have affected recruitment and growth. Interspecific competition (Smith 1970), food supply (Wells 1970), and predation (Smith 1970) might also have influenced recruitment and growth. However, we confined our attention to four hypotheses relating water temperature (Colby 1973) and alewife abundance (Brown 1972) to recruitment and growth. The four hypotheses that could be tested statistically with the available data were as follows.

(1) Recruitment per spawner was inversely related to spawning stock size. Brown (1972) concluded that alewife recruitment at ages 2–4 yr in Lake Michigan varied inversely with adult abundance. This hypothesis that recruitment was density dependent was accepted if the linear regression of the ratio of recruits per spawner (R/P) on parental stock size (P) (Ricker 1975) and $1/R$ on $1/P$ (Beverton and Holt 1957) were significant. In addition, a polynomial regression of recruitment of R on P was done to avoid the problems of autocorrelation inherent in Ricker's (1975) stock–recruitment analysis.

(2) Recruitment per spawner was positively related to water temperature during the year of spawning. Colby (1973) suggested that the failure of the marine alewife to adapt fully to the Great Lakes was partly the result of its inability to adjust to temperature extremes and fluctuations. Edsall (1970) also

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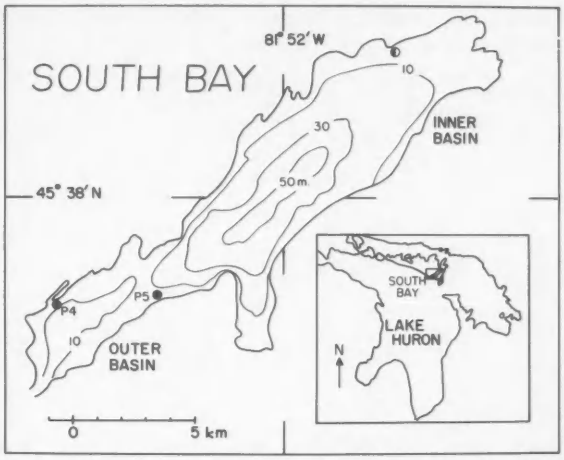

FIG. 1. Location of the poundnets (●) used for sampling alewife in South Bay, Lake Huron, during June 1954–82.

showed that egg survival was reduced below water temperatures of 14°C. We tested this hypothesis by regressing the ratio of recruits to spawners on (a) average temperatures of deep water (54 m) after ice breakup, (b) average water temperatures from May to October in the year of spawning, (c) rate of increase and variability of water temperature in July, and (d) thermal units above 14, 15, and 16°C during spawning in July.

(3) Growth was inversely related to year-class strength and total abundance. Brown (1972) showed that growth and condition of alewives in Lake Michigan were inversely related to abundance. We tested this hypothesis by regressing annual growth rate deviations ($G_d = G - G'$) by age-class on year-class strength (ages 4–6) and total abundance (ages 2–6).

(4) Growth was positively related to water temperature. Colby (1973) described how the schooling and feeding behavior of alewives, and presumably growth, were adversely affected by variations in water temperature. We tested this hypothesis by regressing the deviations of growth rates (G_d) in age intervals 0–1, 1–2, and 2–3 yr on annual average temperatures and by regressing size at age on the average temperatures in the preceding years of the cohort's growth.

Methods

South Bay (Fig. 1) consists of a small outer basin (1361 ha) and a larger inner basin (7490 ha), with average depths of 7.6 and 20.2 m, respectively. Alewife were sampled from the catches of two pound nets (P4, P5) set in the outer basin (1954–82). These pound nets were set and lifted every 2–5 d during June; the cribs, with dimensions of 11 × 11 × 11 m, were set at a depth of 10.5 m and leads were 166 and 205 m long.

The temperature of the water at the deepest location (54 m) in South Bay was recorded on a bathythermograph within the first 2 wk after ice breakup (usually May). Surface-water temperatures were estimated by using McCombie's (1959) equations relating air temperature to surface-water temperatures; air temperatures were recorded at the Fisheries Research Unit on South Bay.

Model 1 regressions are used throughout the analyses (Sokal and Rohlf 1969). Coefficients of determination (r^2) are given for all of the significant regressions, as well as the degrees of freedom used to assess the significance (F-value) of the regression coefficients. Regression equations are not presented because the purpose of the regressions was to test the hypotheses and not to provide predictive models.

Stock Abundance and Structure

The geometric mean number of alewives caught per net-night for all of the lifts made in one net (P4) in June was calculated as an index of stock abundance (catch per unit of effort; CPUE). Only the catches from one pound net were used to estimate CPUE because these catches were larger and less variable than those in the other net; the skewed distribution of catches per lift was corrected by a logarithmic transformation ($\log(e)\ (x + 1)$) (Sokal and Rohlf 1969). Age structure was found by multiplying this index (CPUE) by the proportion of the catch at each age. Ages were determined annually for about 200 alewives by counting annuli on scales viewed on an Eberbach scale projector (1954–70) or through a dissecting microscope (1971–82). Ages were assessed without much difficulty because the annual growth zones were clearly demarcated. Age determinations for the two periods (1954–70 and 1971–82) were done by two different people, but the correlation between the two age assessments of the two readers was high.

We estimated year-class strength as the sum of the CPUEs from age 4, the model age of all catches combined, through age 6 yr and used it as the index of recruitment (R) from the parental stock. Similarly, we used the sum of CPUEs from age 3 to 6 yr as the index of parental abundance (P). By omitting 2-yr-olds we underestimated P, but only a few and highly variable number of 2-yr-olds were captured in the pound nets.

Growth

We based estimates of growth on about 200 empirical measurements of fork length (millimetres) and weight (grams) obtained annually from 1954 to 1982 in the two pound nets. Back-calculations were limited to fish of age 3 because about 80% of the total growth in length had taken place by that age, annuli became increasingly difficult to locate accurately at greater ages, and (most importantly) the sample size that we considered adequate was available for the greatest number of years at age 3. At least 10 age-3 fish of each sex were used in the growth calculations.

From the back-calculated lengths, we computed deviations of observed growth rates (G) from expected rates of growth (G') after obtaining the expected growth rates by regressing $\log(e)$ (Lt/Lt − 1) on initial fork length (Lt − 1). We used the growth rate deviations (G_d) instead of growth increments because annual increments depend on the initial size of the fish at the start of the year, as well as on the suitability of conditions for growth during the year (Jobling 1983).

To obtain an index of condition, we regressed $\log(e)$ (weight, grams) on $\log(e)$ (fork length, millimetres) and divided the estimated weight by the average size of a 3-yr-old male (140 mm). Ten males from each of seven successive 5-mm length groups, starting at 130–134 mm, were used to avoid biases caused by variable length distributions. Males rather than females, were used in this analysis because at the time of sampling (June), the weight of males was less affected by the development of the gonads.

TABLE 1. Catch per unit of effort by age for alewife caught in South Bay (1954–84).

Year	Age 2	3	4	5	6	Σ	Effort (nights set)
1954	18.2	5.5	0.8			24.5	28
1955	183.6	8.1				191.7	30
1956	528.5	122.9	4.1			655.5	27
1957	20.7	11.3	7.7	1.3		41.0	25
1958	2.6	58.1	27.8	2.1	0.4	91.0	29
1959	30.7	175.1	529.8	122.6	8.8	867.0	28
1960	12.1	51.4	220.5	135.9	24.2	444.0	30
1961	1273.0	745.7	784.4	257.2	25.7	3086.0	30
1962	27.9	320.4	408.6	287.7	74.3	1119.0	28
1963	332.9	273.1	793.8	324.4	76.8	1801.0	28
1964	249.6	2329.6	2579.2	637.9	27.7	5824.0	29
1965	227.5	594.9	927.4	253.7	17.5	2021.0	29
1966	195.8	347.1	631.8	275.7	44.5	1495.0	31
1967	24.7	370.7	515.4	176.5	17.7	1105.0	28
1968	155.4	253.5	539.7	171.7	32.7	1153.0	28
1969	260.9	995.6	378.0	202.3	37.3	1874.0	32
1970	137.8	339.2	466.4	74.2	26.5	1044.0	28
1971	45.5	180.2	75.8	23.6	6.7	331.8	30
1972	55.7	286.6	183.1	15.9	15.9	557.3	28
1973	89.9	190.3	153.3	42.0	0.0	475.7	29
1974	27.4	146.0	177.9	82.1	13.	447.2	28
1975	2.9	11.1	16.8	8.2	2.5	41.4	29
1976	104.4	159.2	94.0	39.2	7.8	404.6	29
1977	33.7	27.6	54.4	14.7	6.0	136.3	32
1978	4.9	34.2	21.6	8.4	0.7	69.8	31
1979	57.7	45.3	94.8	103.0	24.7	325.6	28
1980	66.0	167.5	81.2	81.2	10.1	406.1	28
1981	60.3	41.3	45.8	17.9	6.7	171.9	29
1982	4.6	30.8	22.8	7.4	4.0	69.5	29

Results

Stock Size and Recruitment

Relative abundance of the stock (ages 2–6) entering South Bay peaked in 1964 and then declined (Table 1). The geographical distribution of this stock was not studied by tagging and recapturing alewife so that we can only assume that the stock migrates in the Bay during spawning because large numbers of alewife were observed only during June and July. Recruitment (year-class strength) to this stock rose until 1960 and then fell to a sustained low by about 1971 (Table 2). Although the index of early survival (R/P) between egg deposition and full recruitment to the pound nets at age 4 declined initially (1954–61) as parental stock size increased, survival did not improve after the size of the population declined (Table 2). Furthermore, neither the Ricker nor the Beverton and Holt stock–recruitment regression (Ricker 1975) accounted for a significant part of the variation in recruitment ($r^2 = 0.07$ and $r^2 = 0.05$, df = 1,24 and 1,22, respectively; $p > 0.05$). In addition, polynomial regression of recruitment (R) on parental stock size (P) was not significant ($p > 0.05$). We therefore rejected the hypothesis that recruitment was density dependent.

Recruitment and Water Temperature

The index of recruits to parents (R/P) was positively related to average surface-water temperatures (log(e) transformation) from June to October ($r^2 = 0.24$, df = 1,221, $p < 0.025$, Table 2). On a monthly basis, however, this index was a function of water temperatures in only June ($r^2 = 0.28$, df = 1,21, $p < 0.01$) and July ($r^2 = 0.18$, df = 1,21, $p < 0.05$). Variations of R/P were not explained by deepwater temperatures in spring, before alewives spawned ($p > 0.05$), nor with rate of warming before spawning in July ($p > 0.05$), the variability (coefficient of variation) of surface-water temperatures during July ($p > 0.05$) when peak spawning occurred, or the number of degree days above 14, 15, and 16°C in July. Consequently, we accepted the hypothesis that the number of recruits per spawner was positively related to water temperature.

Growth and Abundance

The length at age of alewives declined sharply from 1954 to 1958–59 and then tended to remain low and variable through 1982 (Table 3). The condition index, which also declined from 1954 to 1966 and then remained low (Table 3), was also related to fork length at age 3 ($r^2 = 0.25$, df = 1,27, $p < 0.01$).

Deviations ($G_d = G - G'$) of growth rates of fish in age intervals 0–1 ($p < 0.01$), 1–2 ($p < 0.025$), and 2–3 ($p < 0.025$, df = 1,24) were all inversely related to year-class strength (Table 4); however, growth was not related to the index of total population abundance ($p > 0.05$). The regression of growth rates (G) from time t to $t + 1$ and fork length at time t ($r^2 = 0.88$, df = 1,52, $p < 0.001$, $G = -0.00615L + 0.8972$) was used to estimate expected growth rate (G').

TABLE 2. Year-class strength, spawning stock size, and ratio of recruits to spawners in relation to water temperatures in South Bay.

Year-class	Index of year-class strength (R)	Index of spawning stock, Σ 3–6 yr (P)	Index of R/P	Surface water temperature		
				May–Oct.	June	July
1952	5.8			13.03		
1953	18.6			13.39		
1954	174.5	6.3	27.6	12.59	12.75	16.08
1955	691.5	8.1	85.1	13.86	13.85	18.66
1956	552.0	127.0	4.4	11.71	11.95	14.62
1957	1149.1	20.3	56.6	11.95	11.25	15.02
1958	760.7	88.4	8.6	12.15	10.28	14.89
1959	1449.2	836.4	1.7	12.96	12.28	15.64
1960	2877.4	431.9	6.7	12.50	11.10	14.48
1961	1220.9	1813.0	0.7	12.64	10.87	15.82
1962	841.0	1091.1	0.8	12.51	11.99	16.07
1963	724.4	1468.1	0.5	12.79	12.18	15.42
1964	768.5	5574.4	0.1	12.22	10.55	17.08
1965	458.9	1792.5	0.3	11.57	10.38	13.61
1966	505.9	1299.2	0.4	11.94	10.81	16.94
1967	91.7	1080.3	0.1	11.48	11.80	14.57
1968	239.1	997.6	0.2	12.13	10.23	14.35
1969	237.9	1613.1	0.2	11.78	9.34	15.79
1970	194.0	906.2	0.2	12.30	10.53	15.68
1971	61.9	286.4	0.2	12.28	11.16	14.03
1972	109.3	501.6	0.2	11.57	10.03	14.87
1973	87.5	385.3	0.2	12.65	10.85	16.07
1974	134.8	419.8	0.3	11.41	10.35	16.03
1975	182.7	38.5	4.8	12.85	11.55	16.88
1976	103.0	300.2	0.3	11.76	12.11	15.58

Growth and Water Temperature

Only at age 3 were the fork lengths of both females ($r^2 = 0.26$, df = 1,22, $p < 0.025$) and males ($r^2 = 0.23$, df = 1,23, $p < 0.025$) positively related to average surface-water temperatures (May–October) in the preceding years of growth. Similarly the weight of each sex at age 3 was positively related to these water temperatures (females: $r^2 = 0.29$, df = 1,23, $p < 0.01$; males: $r^2 = 0.026$, df = 1,23, $p < 0.01$). Growth rate deviations (G_d) were a function of water temperature ($r^2 = 0.25$, $p < 0.25$) only in the age interval 1–2. On the basis of these results, we tentatively accepted the hypothesis that growth was influenced by water temperature, but that the effect was probably weak.

Discussion

The decline in abundance of the South Bay alewife stock from its peak in 1964 to the relatively low level of the early 1980s by 1971 was inconsistent with the regulatory action of a stock–recruitment mechanism. Alewife abundance should have increased in the 1970s if a stock–recruitment relation was the main cause for the variations in recruitment. However, we have no information to assess the relative importance of emigration/immigration, species interactions, and predation to the observed variations in alewife numbers.

On the other hand, the significant positive relations between the (index) ratio of recruits to parents and surface-water temperatures in South Bay support the hypothesis that water temperature affects the abundance and probably the distribution of alewives in the Great Lakes. In this regard, Colby (1973) suggested that the alewife had evolved in a marine environment where water temperature is warmer and less variable than in the Great Lakes. The sensitivity of alewife survival to variations in water temperatures may partly explain why alewives are so much scarcer in the cold waters of Lake Superior than in Lakes Michigan (Hatch et al. 1981) and Huron (Argyle 1982). Also, as Smith (1968) suggested, few large alewife populations may exist in Lake Erie because of the dearth of refugia from cold water during the winter, in contrast with the large areas available in the deeper Great Lakes and the ocean.

Variations in surface-water temperatures could also affect larval survival indirectly in several ways. Spawning takes place in littoral waters from at least early July to late August at temperatures of 9–20°C. At these temperatures the eggs hatch within 3–6 d (Mansueti and Hardy 1967). Primary production is a function of water temperature, and to some extent zooplankton production depends on phytoplankton production (Wetzel 1975). Therefore our observed variations in R/P may have been related to water temperature, but mediated through competition for zooplankton. Even if the abundance of zooplankters fluctuates widely, the lowest levels may far exceed the requirements of larval alewives. Alternatively, the abundance of only a few types of small zooplankton (e.g. rotifers and copepods) may be important to the young soon after they hatch at a length of 2.5–5 mm (Auer 1982). Feeding behavior and growth may also be affected by temperature if the metabolism and activity of the larvae are influenced by temperature (cf. Weatherly 1972). As a result, the ability of alewife larvae to catch and use prey optimally may be partly a function of temperature. Any factor

TABLE 3. Empirical fork lengths (mm) and condition index of male alewife sampled in pound nets 4 and 5 in June 1954–82.

Year	Age 2	3	4	5	6	Condition index
1954	158±21(79)	177±14(13)				
1955	144±12(136)	160±26(8)				0.2429
1956	139±15(61)	152±20(16)				0.2214
1957	126±11(44)	156±14(19)	167±13(14)	183±18(2)		0.2286
1958	122±5(3)	138±13(46)	153±13(24)	150±32(2)		0.2143
1959	134±16(3)	134±11(18)	142±14(43)	154±17(9)		0.2000
1960	127(1)	138±9(5)	149±8(25)	149±10(12)		0.2143
1961	116±6(39)	129±5(22)	143±11(21)	147±7(7)		0.2000
1962	121±4(4)	138±9(22)	147±8(34)	156±9(16)	168±8(5)	0.2143
1963	121±6(20)	135±7(26)	139±10(36)	141±7(10)	165(1)	0.1929
1964	125±5(7)	143±8(46)	144±7(39)	148±9(11)		0.2000
1965	127±8(13)	136±8(41)	141±6(49)	147±5(7)		0.2000
1966	118±3(14)	138±8(20)	142±7(12)	141±3(4)	161±14(2)	0.1857
1967	122(1)	137±8(45)	147±6(39)	150±9(14)		0.1929
1968	128±10(10)	140±8(13)	139±21(32)	148±5(6)		0.2000
1969	127±7(31)	135±5(100)	142±7(37)	148±5(10)		0.1929
1970	126±8(21)	138±8(43)	145±5(39)	148±6(7)	147±2(2)	0.2000
1971	126±9(15)	137±8(32)	146±7(8)	156±16(3)		0.1929
1972	129±6(5)	143±7(14)	141±6(12)	149(1)	156(1)	0.2000
1973	133±7(8)	139±5(21)	146±5(6)	146±7(3)		0.2143
1974	141±10(3)	145±9(11)	146±6(20)	151±7(6)		0.2071
1975	137±13(3)	145±7(13)	149±7(24)	150±6(8)	156±7(3)	0.2071
1976	125±7(18)	133±7(22)	138±9(13)	146±11(5)		0.1929
1977	128±5(14)	135±8(19)	141±7(24)	151±7(8)	162±12(2)	0.1929
1978	137±6(2)	134±6(18)	144±7(20)	151±12(5)	150(1)	0.2000
1979	124±9(7)	146±14(6)	152±7(12)	160±5(13)	160±5(4)	0.1929
1980	128±6(6)	134±8(17)	142±2(7)	148±7(6)	153(1)	0.2000
1981	129±7(26)	144±8(16)	144±9(19)	151±4(5)		0.2071
1982	128±3(4)	140±6(28)	146±6(20)	156±8(5)	172(1)	0.1929

that impairs growth may also affect survival if, for example, slow growth extends the time when larvae are vulnerable to predation or to dislocation from suitable nursery habitats by winds and currents.

As noted earlier, Brown (1972) found a negative correlation between somatic growth and total abundance of alewives in Lake Michigan. We, in contrast, found that annual growth rate deviations were not related to total abundance. However, growth rates (G_d) were inversely related to year-class strength. This effect of year-class strength on growth may be a result of competition for food between alewives of similar sizes. It is well known that prey size depends partly on the size of the predator (Checkley 1982; Mittelbach 1981). It has also been hypothesized that competition among similar-sized yellow perch (*Perca flavescens*) explains the inverse relation observed between growth and year-class strength (Henderson 1985). Therefore, the number of fish of a similar size may be more important than total biomass in determining the intensity of competition for food. This possibility is applicable to both inter- and intraspecific interaction (Sheldon et al. 1977).

Although size at age 3 was positively related to temperature in the preceding years of growth, the effect of temperature on growth was probably weak or masked by other variables, because a significant (positive) correlation between growth rate deviations and temperature existed only for age interval 1–2. Water temperature can of course influence fish growth in general (Brett 1979), but the effect of year-class strength on alewife growth was greater than that of temperature.

Alewife recruitment was thus probably more affected by water temperature in South Bay, possibly as a result of hypothesized competition for food, than a stock–recruitment mechanism. Variations in zooplankton and benthic invertebrate production, partly dependent on temperature, may have caused this competition for food, enabling only the faster growing alewives to survive. Competition for food was also intensified by increases in year-class strength. To a much lesser extent, variations in growth were also affected by water temperatures. In South Bay, the effects of relatively cool and variable water temperatures may have obscured any relation between stock size and recruitment. The inverse relation between year-class strength and growth apparently was not strong enough to regulate the size of the stock by adjusting its fecundity.

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TABLE 4. Growth rate deviations of 1952–78 year-classes in relation to year-class strength and water temperature.

Year-class	Age 1–2 G	Age 1–2 $\hat{G}$	Age 1–2 G_d	Age 2–3 G	Age 2–3 $\hat{G}$	Age 2–3 G_d	Year-class strength	R/P	Yearly population size	Temperature (°C) May–Oct. 1953
1952	0.4863	0.3372	0.1491	0.0779	−0.0134	0.0913	5.8	27.6		
1953	0.3844	0.3065	0.0779	0.1326	0.0296	0.0103	18.6	85.1		13.39
1954	0.3800	0.3249	0.0551	0.0777	0.0603	0.0174	174.5	4.4	24	12.59
1955	0.3215	0.3618	−0.0403	0.1324	0.1588	−0.0264	691.5	56.6	191	13.86
1956	0.3930	0.3987	−0.0057	0.1028	0.1588	−0.0560	552.0	8.6	655	11.71
1957	0.3890	0.3926	−0.0036	0.1168	0.1526	−0.0358	1149.1	1.7	41	11.95
1958	0.3298	0.3618	−0.0320	0.0945	0.1526	−0.0581	760.7	6.7	91	12.15
1959	0.2962	0.3618	−0.0656	0.1206	0.1772	−0.0566	1449.2	0.7	867	12.96
1960	0.3578	0.3680	−0.0102	0.1150	0.1403	−0.0253	2877.0	0.8	444	12.50
1961	0.3543	0.3618	−0.0075	0.1141	0.1342	−0.0201	1220.0	0.5	3086	12.64
1962	0.3933	0.3864	0.0069	0.1222	0.1403	−0.0181	841.0	0.1	1119	12.51
1963	0.3215	0.3618	−0.0403	0.1324	0.1588	−0.0264	724.0	0.3	1801	12.79
1964	0.3659	0.3680	−0.0021	0.1213	0.1342	−0.0129	768.0	0.4	5824	12.22
1965	0.3254	0.3372	−0.0118	0.1195	0.1219	−0.0024	458.0	0.1	2021	11.57
1966	0.3813	0.3803	0.0010	0.0930	0.1403	−0.0473	505.0	0.2	1494	11.94
1967	0.3782	0.3618	0.0164	0.0974	0.1157	−0.0183	91.0	0.2	1105	11.48
1968	0.3496	0.3680	−0.0184	0.1232	0.1465	−0.0233	239.0	0.2	1152	12.13
1969	0.3703	0.3618	0.0085	0.1195	0.1219	−0.0024	237.0	0.2	1874	11.78
1970	0.3589	0.3557	0.0032	0.1265	0.1219	0.0046	193.0	0.2	1043	12.30
1971	0.4054	0.3434	0.0620	0.0919	0.0665	0.0254	61.0	0.2	331	12.28
1972	0.3685	0.3311	0.0374	0.1068	0.0788	0.0280	109.0	0.3	557	11.57
1973	0.2988	0.3495	−0.0507	0.1683	0.1588	0.0095	87.0	4.8	475	12.65
1974	0.4467	0.3618	0.0849	0.0289	0.0603	−0.0314	134.0	0.3	447	11.41
1975	0.3115	0.3249	−0.0134	0.0902	0.1157	−0.0255	182.0		41	12.85
1976	0.4092	0.3495	0.0597	0.0925	0.0726	0.0199	103.0		404	11.76
1977	0.3047	0.3618	−0.0571	0.1345	0.1711	−0.0366			136	12.71
1978	0.3489	0.3372	0.0117	0.1169	0.1034	0.0135			69	12.30

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Relative Fishing Power for Canadian Trawlers Landing Pacific Cod (*Gadus macrocephalus*) and Important Shelf Cohabitants from Major Offshore Areas of Western Canada, 1960–81

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Westrheim, S. J., and R. P. Foucher. 1985. Relative fishing power for Canadian trawlers landing Pacific cod (*Gadus macrocephalus*) and important shelf cohabitants for major offshore areas of western Canada, 1960–81. Can. J. Fish. Aquat. Sci. 42: 1614–1626.

Trawling effort was standardized by horsepower class for Canadian trawlers landing Pacific Cod (*Gadus macrocephalus*) and its two principal shelf cohabitants during April–September 1960–81 from the three major offshore regions: southwest Vancouver Island, Queen Charlotte Sound, and Hecate Strait. A linear relationship was demonstrated between landings-per-hour-trawled (LPUE) and vessel horsepower class, with respect to appropriate shelf species groups in each region. Efforts to calculate relative fishing power (RFP) with respect to individual species were frustrated, for one species, by differential depth distribution of effort and abundance. With respect to Pacific cod in northern Hecate Strait, nominal LPUE was shown to underestimate abundance during the 1960s and overestimate abundance in the late 1970s.

On a normalisé l'effort de chalutage déployé d'avril à septembre (1960–1981) selon la catégorie de puissance au frein des chalutiers canadiens exploitant la morue du Pacifique (*Gadus macrocephalus*) et ses deux principaux cohabitants dans les trois grandes régions hauturières : les eaux au sud-ouest de l'île Vancouver, le bassin Reine-Charlotte et le détroit d'Hécate. On a observé une relation linéaire entre les débarquements par heure de chalutage (LPUE) et la catégorie de puissance au frein du bateau relativement aux groupes d'espèces appropriés peuplant la plate-forme dans chaque région. Des écarts de distribution de l'effort et de l'abondance d'une espèce selon la profondeur ont fait échouer les efforts de calcul du potential relatif de pêche (RFP). Pour la morue du Pacifique peuplant le détroit d'Hécate septentrional, on montre que le LPUE nominal sous-estime l'abondance pendant les années 60 et qu'il la surestime vers la fin des années 70.

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Fishing effort is a vital statistic in the assessment of fish stocks. Principal uses are computing an index of stock abundance (LPUE = landings per unit effort) and the instantaneous rate of fishing mortality ($F \cong qE$ = catchability coefficient × effort). If efficiency of fishing vessels increases over time, the use of nominal effort will produce overestimates of abundance, and underestimates of F. Ensuing stock assessments could lead to serious errors in management decisions. Since few substantial fisheries remain static, standardization of effort is essential in most cases. The trawl fishery off western Canada is no exception.

During the last four decades, the Canadian trawl fleet has undergone a number of changes which indicate increasing efficiency: larger vessels (gross tons), increased engine horsepower, improved deck gear, and improved navigation aids and echo sounders (as fish finders). In western Canada, Ketchen and Thomson (1958) initiated effort-standardization studies, and dealt with all species, coastwide. Subsequent studies usually dealt with individual species in localized areas: petrale sole (*Eopsetta jordani*) in area 3C (Ketchen and Forrester 1966), all species in area 4B (Ketchen 1979), Pacific ocean perch (*Sebastes alutus*) in areas 5A and 5B (Ketchen 1981), and rock sole (*Lepidopsetta bilineata*) in area 5D (Forrester and Thomson 1969; Stocker and Fournier 1984) (Fig. 1).

The present study deals with Pacific cod (*Gadus macrocephalus*) and its principal shelf cohabitants off southwest Vancouver Island (area 3C-N) and in Queen Charlotte Sound (areas 5A and 5B) and Hecate Strait (areas 5C and 5D) (Fig. 1). We briefly review the historical progress in effort-standardization methodology, review the results of past studies off western Canada, describe the method we developed, and report the results achieved. Specifically, our method is designed to produce standardized all-species effort required by the Option-2 method (Westrheim 1983) for allotment to individual species in mixed-species trawl fisheries.

Literature Review

Methodology

Gulland (1956) reviewed past methods employed for standardizing effort, defined the concepts of fishing effort and fishing power, and derived a multiplicative model for calculating fishing power of individual English steam and diesel trawlers, and some seiners and pair vessels. He noted that catch was the product of five factors: fishing power, time spent fishing, density of fish, fish vulnerability, and an error term. He found that fishing power was closely correlated with ship length, tonnage,

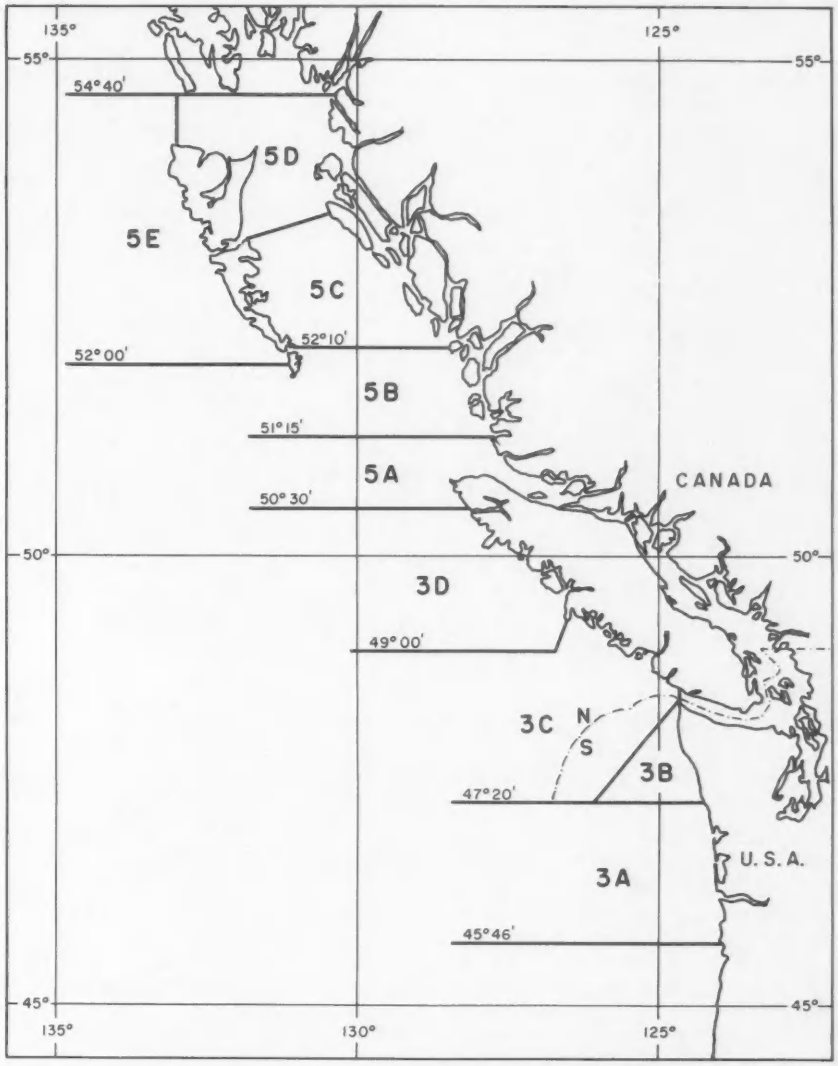

FIG. 1. Major statistical areas for Canada–U.S. trawl landings of groundfish.

and horsepower and that these three factors were also closely correlated with each other. Age of vessel was not critical. Two factors missing, but acknowledged, were "skill of captain and crew" and "equipment of instruments" (probably echo sounders and navigational aids). His results indicated that relative fishing power may vary more among grounds than among species on the same ground.

Beverton and Holt (1957) defined relative fishing power (RFP) and calculated the RFP for individual steam and diesel trawlers fishing for plaice (*Pleuronectes platessa*) in the North Sea. They found that gross tonnage was the most convenient index of fishing power and recommended as the standard unit of fishing effort thousands of steam trawler ton-hours per year.

Rounsefell (1957) developed a method for computing standardized catch per fishing day for U.S. otter trawlers operating on Georges Bank in the western Atlantic. Catch rates were standardized, per individual vessel, using the ratio of engine horsepower to length and age of vessel. Tonnage class was not a factor. The unique discovery of this analysis was the need to segregate catches by depth interval fished and species caught.

Robson (1966) reviewed the four alternative estimates of fishing power per vessel of Beverton and Holt (1957) and demonstrated that a fifth alternative was more efficient. He concluded that "Most efficient statistical procedure for estimating and testing various factors affecting fishing power is the method of least squares regression analysis, or, equivalently, the factorial analysis of variance for unequal sub-class numbers." However, as noted by Gulland (1956), statistical relevance depends heavily on experimental design.

Pope (1975) reviewed current methods employed to standardize effort. Notable in the review were papers contributed, possibly for the first time, by economists. One (Carlson 1975)

TABLE 1. Factors employed, or suggested, by other studies on effort standardization and their relationship to the current study.

Factor	Other studies	Current study
1. Species	Usually individual	Species groups
2. Vessels	Usually individual	Vessel groups; horsepower classes
3. Propulsion type	Usually omitted	Omitted; not applicable
4. Location	Usually individual grounds	Statistical area(s), combined grounds
5. Depth	Usually omitted	Omitted; study applies only to shelf species
6. Time	Seasonal, usually monthly intervals	April–September 1960–81 Monthly variation in LPUE deemed modest
7. Qualification level	Usually omitted	Constant 80% for species groups
8. Deck gear	Usually omitted	Omitted; one gear class (double + drum) predominated
9. Trawl gear	Usually omitted	Omitted; available data incomplete
10. Navigational aids and echo sounder	Suggested	Omitted; available data not quantifiable
11. Vessel captain	Suggested	Omitted; available data incomplete
12. Economics	Suggested	Omitted; data not available

reported that "total production and total value in some mixed fisheries which have been studied are capable of a high degree of explanation in terms of fishing power and fishing time statistics."

Kimura (1981) developed a log-linear (multiplicative) model that "allows the calculation of two standardized abundance indices: (1) direct interpretation of regression coefficients for the year factor; and (2) the usual estimates of CPUE calculated from standardized effort (adjusted C.P.U.E.)." The technique was applied to two Pacific ocean perch (*Sebastes alutus*) stocks off British Columbia, using records of those U.S. trawlers whose captains responded to a questionnaire on fishing equipment utilized. He reported that the regression coefficient estimates have advantages in theoretical simplicity and computational convenience. However, the two methods did not always produce similar results.

Stocker and Fournier (1984) expanded on Kimura's (1981) method by including percentage target species catch as well as vessel characteristics in the multiplicative fishing power model. They applied the method to rock sole landed from the Two Peaks – Butterworth Ground in Hecate Strait (area 5D) by individual Canadian trawlers during June–September 1954–78. Notably, they tested the usefulness of their standardized CPUE in a dynamic version of the Schaefer surplus production model (Schnute 1977) by comparing predicted catch (actually landings) based on standardized and nominal CPUEs. They concluded that standardizing effort did not appreciably improve the predictions.

In summary, the most effective, and statistically sound, method for standardizing effort is the log-linear, multiplicative model applied to individual vessels. As Gulland (1956) noted, statistical relevance requires that among-vessel comparisons must be made in restricted area–time cells. Advances in computer technology have led to more sophisticated analyses (Robson 1966; Kimura 1981; Stocker and Fournier 1984), but the general principles enunciated by Gulland (1956) remain relevant.

With respect to factors affecting trawler efficiency, 12 have been noted in this brief review (Table 1). None is universally applicable. Hence, for each investigation, a careful review of the available (and unavailable!) factors is essential to ensure a satisfactory standardization of fishing effort.

Regional Results

Off western North America, the first report on trawl effort standardization was that of Ketchen and Thomson (1958). They created seven tonnage classes for Canadian single- and double-gear trawlers[1] landing groundfish during 1955–57. All-species LPUEs were standardized to tonnage class 3 (25–49 t), double-gear vessels. RFP values among tonnage classes for double-gear vessels ranged from 0.22 (tonnage class 1, <15 t) to 1.46 (tonnage class 6, >99 t).

Ketchen and Forrester (1966) standardized LPUEs for the "southern" stock of petrale sole resident on the continental shelf off southwest Vancouver Island (area 3C) during May–August

[1]Single-gear vessels tow the trawl with a single warp and bridle off one side of the vessel. Double-gear vessels tow the trawl with twin warps off the stern quarters of the vessel.

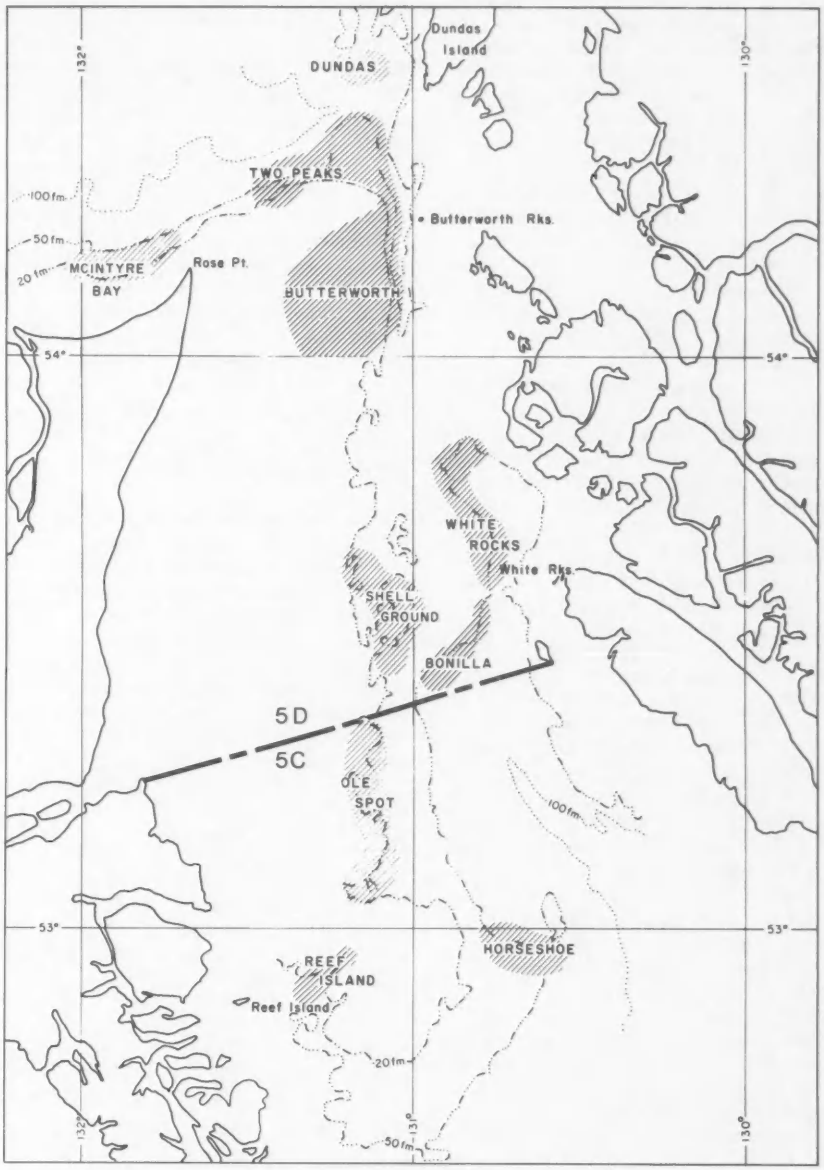

FIG. 2. Important shelf trawling grounds in Hecate Strait.

1945–63. Standard vessel was tonnage 10–49, single-gear. Double-gear vessels, of the same tonnage class, were deemed to be 1.5 times as efficient as single-gear vessels. There was no trend in tonnage class during the study period.

Forrester and Thomson (1969) standardized LPUEs (pounds per day fished; 50% qualification level) for rock sole by Canadian trawlers operating on Butterworth Ground in Hecate Strait (Fig. 2) during May–October 1945–59. They reported that LPUEs for double-gear vessels were 1.4 times those of single-gear vessels during 1949–52 when both gear classes were well represented in the fishery. They noted that there was no trend in tonnage class during the study period.

Chikuni (1975) reported a dome-shaped relationship between CPUE and vessel tonnage class for Japanese stern trawlers fishing Pacific ocean perch in the British Columbia – Oregon region, and three other regions northward to the eastern Bering Sea. Modal tonnage class was 8 (2500–3499 t), and using this as a standard, minimal RFPs were ~0.2 for the smallest class (3; 300–499 t) and ~0.6 for the largest (9, >3499 t) (Chikuni 1975, table 19, fig. 45).

Ketchen (1979) standardized Canadian trawling effort for "foodfish" (species landed for human consumption) caught in the Strait of Georgia (area 4B) (Fig. 1) during October–March 1954–78 by all vessels, to tonnage class 3, double-gear, in order

to undertake a general analysis of the landing statistics of this complex fishery. For the standard class, RFP was 1.4 times that of tonnage class 3, single-gear, the other important vessel class in operation during the study period. This ratio was computed as a grand average, ignoring among-year variations.

Ketchen (1981) used a modified power factor of Beverton and Holt (1957) to standardize Canadian trawling effort for Pacific ocean perch in Queen Charlotte Sound (areas 5A and 5B) (Fig. 1). Restraints were a qualification level (60%), minimum depth (85 fathoms), and time (monthly, May–December). Tonnage class 7 (150–199 t) was selected as the standard class. Relationship between power factor and tonnage class varied substantially among years, as did the number of tonnage classes involved. However, mean values exhibited a steady increase from 0.89 for tonnage class 6 (100–149 t) to 1.36 for tonnage class 9 (300–399 t). Only four tonnage classes were important components during the study period.

Kimura (1981) chose three variables (gross tonnage, acoustic echo sounders with paper recorders, and roller (bobbin) gear) for application to a selected group of U.S. vessels trawling for Pacific ocean perch in two regions (areas 3C and 5A + 5B) (Fig. 1) off British Columbia during 1953–76, and two qualification levels (0 and 25%) to calculate CPUEs (actually LPUEs). He noted interregional differences in the significance of the three selected factors and concluded that technological improvements had a greater effect (two times) on LPUEs for depleted stocks (off Vancouver Island) than for those in "good" condition (Queen Charlotte Sound). An equally plausible explanation is that the contrasting ocean perch habitat was the cause. That is, off Vancouver Island, the ocean perch occupy the steep, irregular, and poorly charted continental slope, most of which is untrawlable, where bobbins are essential and to a lesser extent recording echo sounders (Westrheim 1970). In contrast, the ocean perch habitat in Queen Charlotte Sound is a broad, gently sloping gully, some 86% of which is trawlable (Westrheim 1974). Kimura (1981) further noted that the choice of qualification level was critical off Vancouver Island where abundance declined substantially, but was not critical in Queen Charlotte Sound where abundance declined moderately. A plausible explanation can be found in the rockfish species complexes of the two study areas. Off Vancouver Island, numerous rockfish species cohabit on the continental slope (Westrheim 1970), while in Queen Charlotte Sound, Pacific ocean perch generally comprise approximately 90% of the rockfish catch in the area they are sought (Westrheim 1974). Kimura (1981) did note appropriately that "the problem of how qualification levels should be applied also needs to be examined. It would seem that a sound rationale for their use (if they should be used at all) would be helpful."

Johnson et al. (1982) analyzed the 1978–79 landing statistics of the Oregon trawl fleet. They compared LPUEs of five species categories (all species, all rockfish, all flatfish, all roundfish, and Dover sole (*Microstomus pacificus*)) with vessel length, tonnage, and horsepower. Regressions of landed catch per days fished and landed catch per trip on vessel size classifications were significant, but usually explained less than half the variance. They concluded that variance was too high to delineate meaningful differences in LPUE among vessel classifications.

Stocker and Fournier (1984) employed six tonnage classes (<25, 25–49, 50–74, 75–99, 100–199, and >199), three gear types (single, double, and double + drum), and a qualification level of 25% for Canadian landings of rock sole from Two Peaks – Butterworth Ground during June–September 1954–78 (Fig. 2). They concluded that tonnage class had "no significant effect on the observed catch levels for rock sole in northern Hecate Strait." Their "test" of relevance of rock sole effort standardization utilized a catch forecast model that they and others (Stocker and Hilborn 1981) deemed to be of limited value.

In summary, RFPs for Canadian vessels varied among gear classes (single vs. double), with tonnage class constant, and linearly among tonnage classes, with gear class constant. In all cases, tonnage class range was relatively small. For Japanese trawlers, with a substantial range of tonnage, a dome-shaped relationship was demonstrated between CPUE and tonnage class. Furthermore, considerable variability can be expected in RFP data. Pitfalls in interpretation of RFP analysis were noted in two cases, where additional detailed knowledge of the species' fishery, bathymetric distribution, assemblage, and/or habitat provided alternative, and plausible, conclusions.

Materials and Methods

Data used in this analysis included only landing records collected by Port Liaison Officers, who interview Canadian trawler captains when catches are landed for sale. These "interviewed" landings comprise at least 70% of the annual trawl landings. Each record includes name of vessel, date of landing, location(s) trawled (major area, minor area, ground), depth range trawled, time trawled (nominal effort), and weight of each species retained for sale. Continuing records are maintained for each vessel of its tonnage, main engine horsepower, deck gear, and the presence or absence of navigational aids (RDF, RADAR, LORAN, and echo sounder).

The underlying model for deriving relative fishing power is that of Gulland (1956, p. 5):

$$Y_{ij} = P_i \times t_{ij} \times D_j \times \alpha_j \times E_{ij}$$

where Y_{ij} = catch of vessel i in position and period j, P_i = (absolute) fishing power of vessel i, t_{ij} = time spent fishing by vessel i in position and period j, D_j = density of fish in position and period j, α_j = vulnerability of fish in position and period j, and E_{ij} = random variable (E_{ij} is not quantifiable in the present study and is therefore omitted).

Gulland noted that absolute fishing power is rarely calculable, because D_j is rarely measurable directly. The product of $D_j \times \alpha_j$ is then estimated by the LPUE (Y_{sj}/t_{sj}) of a "standard" vessel.

The calculation of RFP follows (using the terminology of the current study):

$$\text{RFP}_i = (\text{LPUE}_{ij})/(\text{LPUE}_{sj})$$

where $\text{LPUE}_{ij} = Y_{ij}/t_{ij}$ and $\text{LPUE}_{sj} = Y_{sj}/t_{sj} \cong (D_j)\ (\alpha_j)$.

Gulland's subsequent analyses involved log-transformed data whose variability was demonstrated to be reasonably normal with constant variance.

Available data for our study did not warrant comparison of individual vessels in restricted area–time cells. Hence, the log-linear multiplicative model offered no apparent advantage over a simple linear regression model relating, in this case, LPUE to horsepower class for selected species groups in relatively broad area–time cells.

Species

Initial analyses involved individual, important shelf species on each major trawling ground. Anomalous results for data from

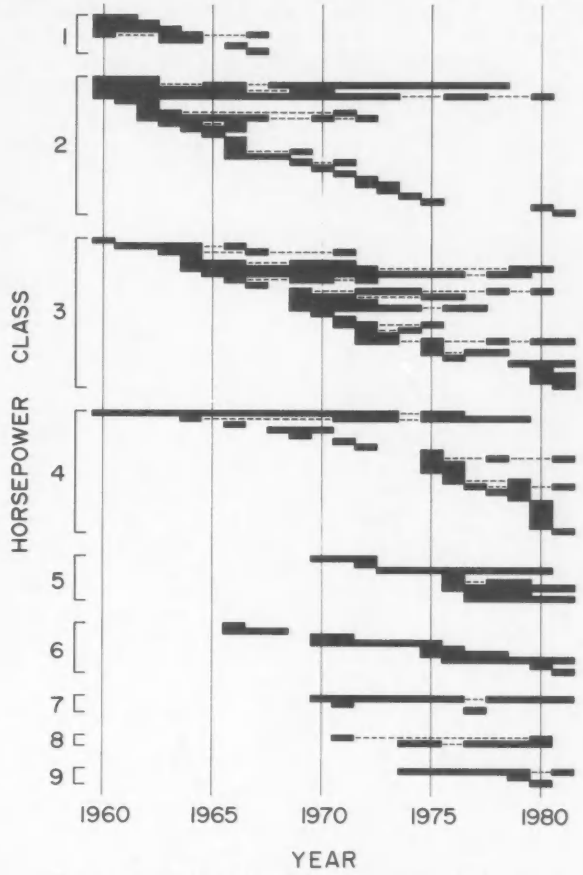

FIG. 3. Incidence of individual Canadian trawlers, by horsepower class and year, landing selected shelf species from area 3C-N during April–September 1960–81.

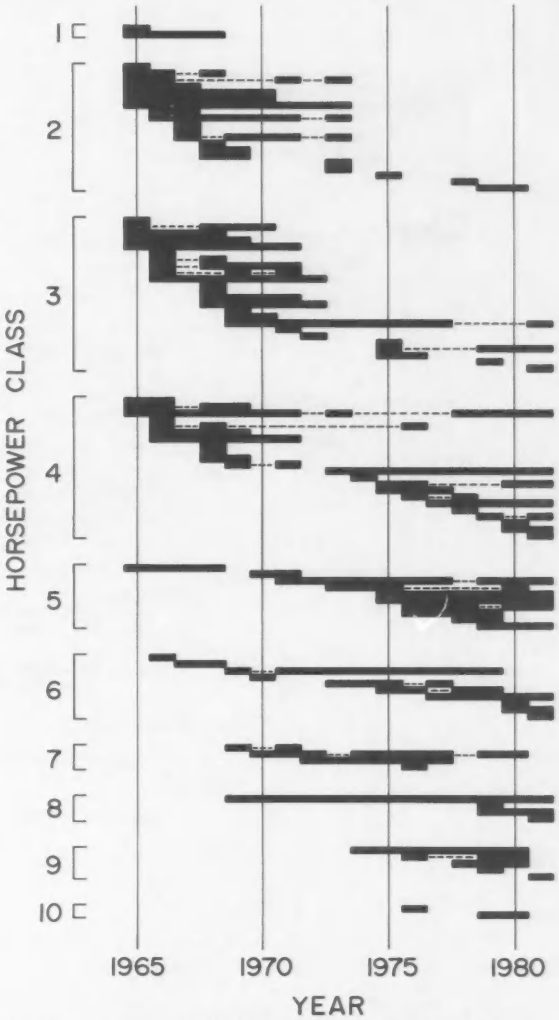

FIG. 4. Incidence of individual Canadian trawlers, by horsepower class and year, landing selected shelf species from areas 5A + 5B during April–September 1960–81.

Two Peaks – Butterworth Ground (area 5D) led to the creation of species groups on each location consisting of Pacific cod and its two important shelf cohabitants: lingcod (*Ophiodon elongatus*) and petrale sole in area 3C-N, lingcod and rock sole in Queen Charlotte Sound (areas 5A and 5B), and rock sole and English sole (*Parophrys vetulus*) in Hecate Strait (areas 5C and 5D). Use of these species groups is reasonable, because they are customarily caught together (Westrheim and Foucher 1985).

Vessels

Analysis by individual vessels was precluded by their transitory nature. No vessel produced landings from any region during the entire study period, and many trawled only 1–3 yr (Fig. 3–5). Therefore, the vessels were classified by tonnage class (50-t intervals) and main-engine horsepower class (100-hp intervals). Most vessels trawled in at least two regions in any year.

Initially, both tonnage and horsepower classes were considered as factors. For Pacific cod from Two Peaks – Butterworth Ground (April–September 1960–81), regression parameters for LPUE on tonnage and horsepower indicated close relationships in both cases:

	Parameters		
LPUE on:	a	b	R^2
Tonnage class	40.2	29.9	0.94
Horsepower class	15.6	24.3	0.79

However, tonnage class was rejected, because mean horsepower increased substantially over time within tonnage classes (Table 2). Within horsepower classes, mean tonnage was stable, or declined moderately, over time (Table 3).

A total of 158 individual vessels were involved in the analysis (Table 4), and 29 of these changed horsepower by one class and 6 by two classes (Table 5).

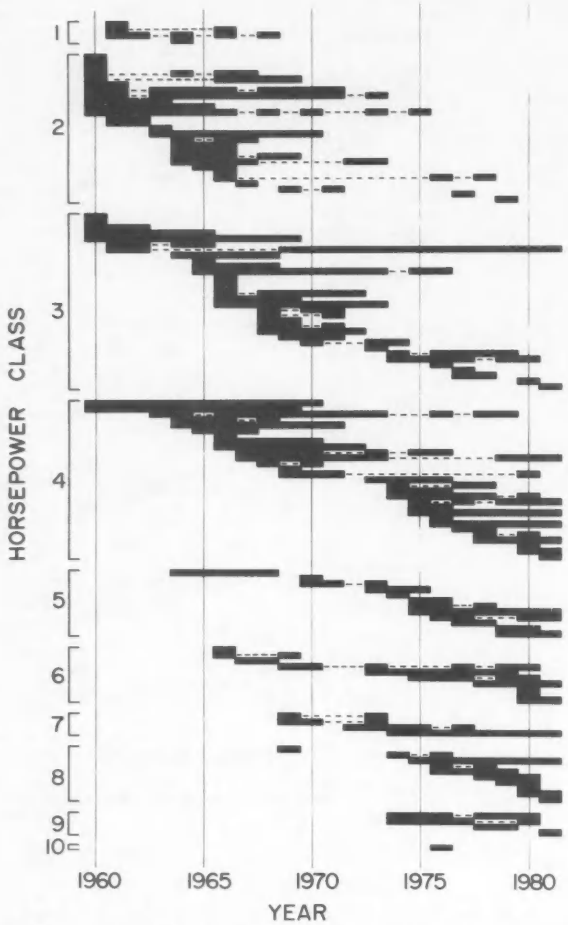

FIG. 5. Incidence of individual Canadian trawlers, by horsepower class and year, landing selected shelf species from areas 5C + 5D during April–September 1960–81.

Location

Initial analyses involved individual important trawling grounds. Anomalous results for Two Peaks – Butterworth Ground in Hecate Strait led to consolidating landing statistics by individual or grouped major statistical areas: 3C-N, 5A + 5B, 5C, and 5D (Fig. 1). The separation of Hecate Strait by major area was precautionary due to incomplete stock delineation.

Time

Records for April–September 1960–81 were selected for analysis. Among-season variations in behaviour of species and vessels precluded use of records for autumn and winter. In Hecate Strait and off southwest Vancouver Island, LPUEs for Pacific cod during October–March do not reflect abundance, and hence are not used in stock assessments (Foucher and Westrheim 1984). In Queen Charlotte Sound, virtually no trawling occurs on the continental shelf during October–March (Foucher and Westrheim 1984). Records prior to 1960 were excluded because (1) Pacific cod was in low demand among Canadian processors, (2) single-gear trawlers had largely been

TABLE 2. Mean horsepower, by selected tonnage class, of Canadian trawlers landing selected species[a] from areas 3C-N, 5A + 5B, and 5C + 5D during April–September by 5-yr intervals, 1960–81.

Area	Year				
	1960–64	1965–69	1970–74	1975–79	1980–81
Tonnage class 1 (<49 t)					
3C-N	142	174	197	257	225
5A + 5B	—	181	195	210	225
5C + 5D	128	173	224	207	230
Tonnage class 2 (50–99 t)					
3C-N	207	203	242	309	333
5A + 5B	—	231	258	322	375
5C + 5D	208	248	284	337	346
Tonnage class 3 (100–149 t)					
3C-N	—	393	523	483	544
5A + 5B	—	388	473	460	492
5C + 5D	279	388	445	519	534
Tonnage class 4 (150–199 t)					
3C-N	—	—	521	543	565
5A + 5B	—	447	517	608	593
5C + 5D	400	502	542	615	645

[a]3C-N, Pacific cod + lingcod + petrale sole; 5A + 5B, Pacific cod + lingcod + rock sole; 5C + 5D, Pacific cod + English sole + rock sole.

TABLE 3. Mean gross tonnage, by selected horsepower class, of Canadian trawlers landing selected species[a] from areas 3C-N, 5A + 5B, and 5C + 5D during April–September by 5-yr intervals, 1960–81.

Horse-power class	Year				
	1960–64	1965–69	1970–74	1975–79	1980–81
Horsepower class 2 (100–199 hp)					
3C-N	39	44	44	53	35
5A + 5B	—	46	47	52	48
5C + 5D	47	46	48	47	—
Horsepower class 3 (200–299 hp)					
3C-N	45	52	48	50	49
5A + 5B	—	59	49	58	44
5C + 5D	87	66	59	63	74
Horsepower class 4 (300–399 hp)					
3C-N	59	68	70	78	70
5A + 5B	—	88	80	88	87
5C + 5D	85	88	77	79	76
Horsepower class 5 (400–499 hp)					
3C-N	—	—	145	104	113
5A + 5B	—	166	145	105	108
5C + 5D	166	166	150	103	103
Horsepower class 6 (500–599 hp)					
3C-N	—	132	171	158	128
5A + 5B	—	143	174	156	134
5C + 5D	—	149	174	149	146

[a]3C-N, Pacific cod + lingcod + petrale sole; 5A + 5B, Pacific cod + lingcod + rock sole; 5C + 5D, Pacific cod + English sole + rock sole.

TABLE 4. Numbers of Canadian trawlers, by horsepower class, included in calculations of relative fishing power, by location of catch.

Horsepower class	Origins of landings			
	3C-N[a]	5A + 5B[b]	5C + 5D[c]	Total[d]
1	7	2	5	12
2	25	20	25	44
3	27	24	32	45
4	22	22	29	43
5	8	11	12	13
6	9	11	10	13
7	3	4	4	4
8	2	4	10	11
9	3	5	4	4
10	—	2	1	2
Total	106	105	132	158

[a]Among-year arrays shown in Fig. 3.
[b]Among-year arrays shown in Fig. 4.
[c]Among-year arrays shown in Fig. 5.
[d]Actual numbers of individual vessels involved in this study.

TABLE 5. Numbers of Canadian trawlers, by horsepower class, included in this study that changed horsepower class during the study period.

Original horsepower class	Change in horsepower class			
	+1	+2	+1/+1[a]	Total
1	2	3	1	6
2	7	3	1	11
3	6	—	1	7
4	1	—	—	1
5	3	—	—	3
6	1	—	—	1

[a]Two changes: +1 class each.

phased out by 1960, and (3) uncorrectable encoding errors (for trawling grounds) were discovered in some landings prior to 1960.

Among-month variation in LPUEs, during April–September 1960–81, were deemed too modest to warrant consideration of intrayear comparisons. This can be seen in Fig. 6, where we converted monthly species group LPUEs (and landings) to percentages of April–September sums in each year, and then calculated among-year mean percentages for each month.

Excluded Factors

The remaining factors from Table 1 not included as variables in the current analysis are propulsion type, depth, qualification level, deck gear, trawl gear, navigational aids and echo sounders, vessel captain, and economics. *Propulsion* was not relevant, as all vessels were diesel powered. *Depth* was omitted because in each region, the three principal shelf species occupy a common and relatively narrow depth range, 10–59 fathoms (18–108 m), for Two Peaks – Butterworth Ground (e.g. see Westrheim 1983). *Qualification level* was treated as a constant (80%) in order to exclude occasional, but substantial, landings

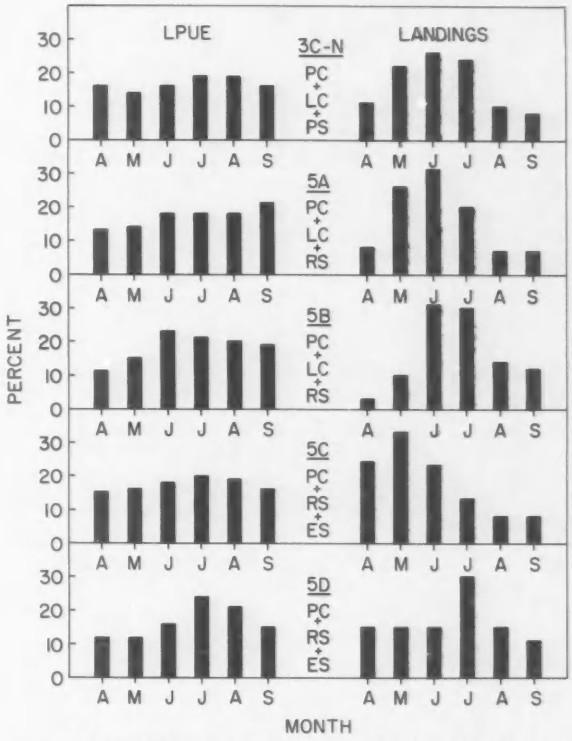

FIG. 6. Mean distribution (%) of LPUEs and landings of shelf species groups, by month by major area, during April–September 1960–81. ES, English sole; LC, lingcod; PC, Pacific; PS, petrale sole; RS, rock sole.

of extraneous species such as arrowtooth flounder (*Atheresthes stomias*), rockfish (*Sebastes* sp.), spiny dogfish (*Squalus acanthias*), and walleye pollock (*Theragra chalcogramma*). *Deck gear* was omitted, because one gear class (double + drum) predominated during the study period. The remaining potential factors (trawl gear, navigational aids and echo sounder, vessel captain, and economics) were omitted, because appropriate data were unquantifiable, incomplete, or unavailable.

To recap,the current study utilizes species groups, horsepower classes, major statistical areas, and a fixed time period. Only horsepower class was treated as a variable.

LPUE Computations

For individual species, the Option-2 method[2] (Westrheim 1983) was employed to calculate LPUE. For species groups, the conventional qualification method[3] was employed, at the 80% level.

[2]Arrange landings of individual species, and all-species effort, by depth intervals; select depth intervals containing the rank-1 and rank-2 landings; assign all-species effort from the same two depth intervals to the species in question.

[3]Total effort for an individual trip, or identifiable portion thereof, is allotted to each species accounting for at least a specified percentage (qualification level) of the landing in question. LPUE = (qualified landings)/(qualified effort).

TABLE 6. Pacific cod fishing parameters, by horsepower class and year, for Option-2 depth int

Horsepower class	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Landings (t)										
1 (0–99)	—	33	—	—	5	—	5	—	1	—
2 (100–199)	91	289	229	49	291	84	347	14	37	18
3 (200–299)	176	50	54	117	346	440	603	293	192	68
4 (300–399)	114	—	18	222	616	480	746	225	147	373
5 (400–499)	—	—	—	—	237	226	114	60	132	—
6 (500–599)	—	—	—	—	—	—	94	—	6	30
7 (600–699)	—	—	—	—	—	—	—	—	—	—
8 (700–799)	—	—	—	—	—	—	—	—	—	—
9 (800–899)	—	—	—	—	—	—	—	—	—	—
10 (900+)	—	—	—	—	—	—	—	—	—	—
Total	381	372	301	388	1495	1230	1909	592	515	489
Effort (h)										
1 (0–99)	—	60	—	—	35	—	36	—	10	—
2 (100–199)	297	573	399	233	200	105	317	15	49	89
3 (200–299)	298	194	151	179	201	273	435	239	540	237
4 (300–399)	87	—	44	308	267	174	596	210	235	586
5 (400–499)	—	—	—	—	58	51	81	45	146	—
6 (500–599)	—	—	—	—	—	—	68	—	2	96
7 (600–699)	—	—	—	—	—	—	—	—	—	—
8 (700–799)	—	—	—	—	—	—	—	—	—	—
9 (800–899)	—	—	—	—	—	—	—	—	—	—
10 (900+)	—	—	—	—	—	—	—	—	—	—
Total	682	827	594	720	761	603	1533	509	982	1008
LPUE (kg/h)										
1 (0–99)	—	548	—	—	133	—	138	—	58	—
2 (100–199)	305	503	574	209	1455	800	1093	905	761	204
3 (200–299)	591	257	360	653	1719	1610	1385	1224	355	284
4 (300–399)	1309	—	418	719	2308	2758	1252	1071	627	636
5 (400–499)	—	—	—	—	4084	4426	1411	1323	902	—
6 (500–599)	—	—	—	—	—	—	1389	—	3175	307
7 (600–699)	—	—	—	—	—	—	—	—	—	—
8 (700–799)	—	—	—	—	—	—	—	—	—	—
9 (800–899)	—	—	—	—	—	—	—	—	—	—
10 (900+)	—	—	—	—	—	—	—	—	—	—
Mean	559	450	507	539	1965	2040	1245	1163	524	485
No. of landing records										
1 (0–99)	—	5	—	—	5	—	1	—	1	—
2 (100–199)	28	43	33	12	23	10	25	1	4	7
3 (200–299)	18	12	7	7	8	16	26	18	34	20
4 (300–399)	6	—	3	15	21	11	36	20	20	36
5 (400–499)	—	—	—	—	3	4	4	2	7	—
6 (500–599)	—	—	—	—	—	—	4	—	1	4
7 (600–699)	—	—	—	—	—	—	—	—	—	—
8 (700–799)	—	—	—	—	—	—	—	—	—	—
9 (800–899)	—	—	—	—	—	—	—	—	—	—
10 (900+)	—	—	—	—	—	—	—	—	—	—
Total	52	60	43	34	60	41	96	41	67	67

depth intervals on Two Peaks – Butterworth Ground, April–September 1960–81.

1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Total
—	—	—	—	—	—	—	—	—	—	—	—	—	44
18	14	55	—	—	—	—	55	—	2	5	—	—	1 580
68	114	165	357	542	253	289	140	428	93	105	52	17	4 894
373	97	134	228	292	169	50	73	36	36	202	33	71	4 362
—	5	—	—	—	231	34	15	—	—	99	108	141	1 402
30	—	—	—	—	3	25	24	76	85	210	119	256	928
—	—	—	—	—	280	256	58	106	—	38	41	12	791
—	—	—	—	—	—	434	268	670	97	396	368	247	2 480
—	—	—	—	—	131	—	—	—	—	—	—	—	131
—	—	—	—	—	—	—	—	—	—	—	—	—	—
489	230	354	585	834	1067	1088	633	1316	313	1055	721	744	16 612
—	—	—	—	—	—	—	—	—	—	—	—	—	141
89	291	274	—	—	—	—	153	—	28	49	—	—	3 072
237	349	598	732	664	387	496	443	1116	531	388	251	130	8 832
586	242	460	321	243	105	107	211	106	293	415	112	298	5 420
—	28	—	—	—	104	36	116	—	—	219	201	354	1 439
96	—	—	—	—	34	21	37	93	141	524	407	904	2 327
—	—	—	—	—	171	265	181	145	2	94	83	78	1 019
—	—	—	—	—	—	323	305	1062	478	454	302	493	3 417
—	—	—	—	—	54	—	10	—	—	—	—	—	64
—	—	—	—	—	—	—	—	—	—	—	—	—	—
1008	910	1332	1053	907	855	1248	1456	2522	1473	2143	1356	2257	25 731
—	—	—	—	—	—	—	—	—	—	—	—	—	
204	49	202	—	—	—	—	362	—	79	104	—	—	
284	325	276	487	816	654	582	316	383	175	269	207	134	
636	402	292	709	1199	1614	470	346	344	123	485	292	237	
—	164	—	—	—	2221	954	127	—	—	449	536	398	
307	—	—	—	—	79	1196	646	814	603	401	292	283	
—	—	—	—	—	1635	964	322	732	32	399	488	155	
—	—	—	—	—	—	1343	877	630	202	873	1219	501	
—	—	—	—	—	2417	—	36	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	
485	253	266	556	920	1248	872	435	522	212	492	532	330	
—	—	—	—	—	—	—	—	—	—	—	—	—	12
7	15	17	—	—	—	—	11	—	2	8	—	—	239
20	35	45	42	39	25	29	20	66	32	23	16	8	546
36	27	36	24	25	12	14	12	5	21	25	15	16	400
—	3	—	—	—	5	2	3	—	—	18	16	19	86
4	—	—	—	—	1	2	2	4	7	26	29	37	117
—	—	—	—	—	13	28	17	8	1	8	4	3	82
—	—	—	—	—	—	20	19	39	19	17	22	30	166
—	—	—	—	—	1	—	2	—	—	—	—	—	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—
67	80	98	66	64	57	95	86	122	82	125	102	113	1 651

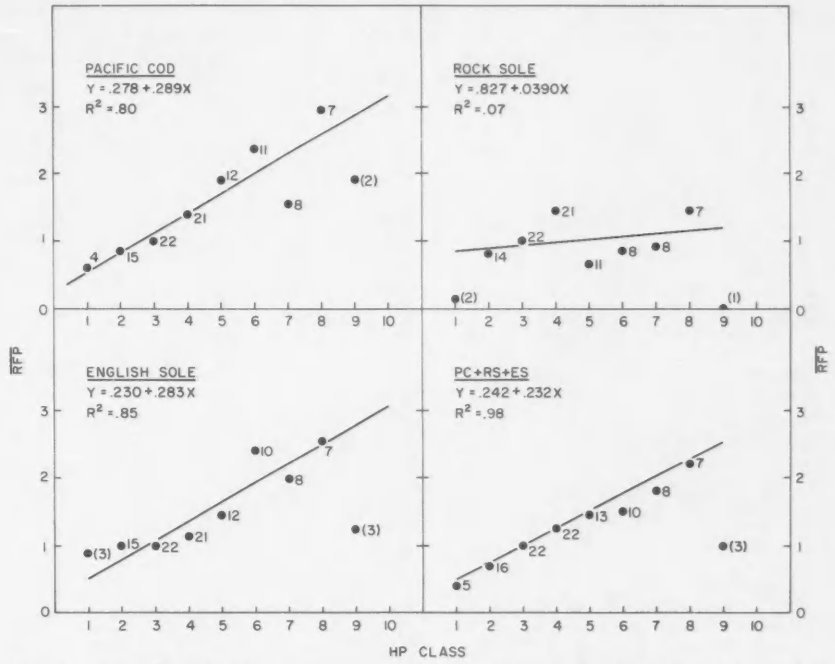

FIG. 7. Regressions of RFP on horsepower class for selected shelf species landed by Canadian trawlers from Two Peaks – Butterworth Ground.

RFP Computation

Estimation of RFP by horsepower class is completed in four steps. We demonstrate the method as follows, using as an example the initial analysis of Pacific cod data for Two Peaks – Butterworth Ground (area 5D) during April–September 1960–81.

Step 1: Compile landings, nominal effort, and LPUE by horsepower class by year. Data for our example are contained in Table 6.

Step 2: Select standard horsepower class on the basis of number of data years in the time series, cumulative weight of landings, cumulative effort expended, and cumulative numbers of landing records. In our example, horsepower class 3 was selected as the standard, because its time series included the entire study period (Table 6), and it produced the largest cumulative landings (4874 t, 42%), cumulative effort (8832 h, 34%), and numbers of landing records (546, 33%).

Step 3: Calculate mean RFP for each horsepower class:

$$\overline{\mathrm{RFP}_i} = \frac{1}{n_i} \sum_{j=1}^{n_i} (\mathrm{LPUE}_{ij}/\mathrm{LPUE}_{sj})$$

where RFP_i = mean relative fishing power for horsepower class i, n_i = number of years of records for horsepower class i, LPUE_{ij} = LPUE for horsepower class i in year j, and LPUE_{sj} = LPUE for the standard horsepower class in year j.

In our example, the $\overline{\mathrm{RFP}}$ values for horsepower classes 1–9 are (n_i in parentheses) 0.618 (4), 0.866 (15), 1.000 (22), 1.399 (21), 1.911 (12), 2.348 (11), 1.533 (8), 2.965 (7), and 1.905 (2).

By effectively setting each LPUE_{sj} to 1, annual variations in cod abundance are accounted for as well as variations in the distribution of effort among horsepower classes from year to year.

Step 4: Regress $\overline{\mathrm{RFP}}$ on horsepower class to correct for horsepower classes with small values of n_i and recalibrate to the standard horsepower class 3:

$$\widehat{\overline{\mathrm{RFP}}}_i' = a + b \text{ (horsepower class } i)$$

$$\widehat{\overline{\mathrm{RFP}}}_i = \widehat{\overline{\mathrm{RFP}}}_i'/\widehat{\overline{\mathrm{RFP}}}_s'$$

where $\widehat{\overline{\mathrm{RFP}}}_i'$ = uncalibrated estimate of relative fishing power for horsepower class i, a and b = regression parameters, $\widehat{\overline{\mathrm{RFP}}}_i$ = calibrated estimate of RFP for horsepower class i, and $\widehat{\overline{\mathrm{RFP}}}_s'$ = uncalibrated estimate of RFP for the standard class.

In our example, the regression excluded horsepower classes 1 ($n = 4$) and 9 ($n = 2$). Regression parameters were $a = 0.233$ and $b = 0.296$ ($R^2 = 0.73$). $\overline{\mathrm{RFP}}$ values for horsepower classes 1–10 were 0.47, 0.74, 1.00, 1.27, 1.53, 1.79, 2.06, 2.32, 2.59, and 2.84, respectively.

Results

Individual Species

For Two Peaks – Butterworth Ground, regressions of $\overline{\mathrm{RFP}}$ on horsepower class were linear for Pacific cod, English sole, and the three-species cod–sole group; R^2 values were 0.80, 0.85, and 0.98, respectively (Fig. 7). The rock sole regression produced a poor fit ($R^2 = 0.07$) and indeed the array suggested two regressions, one for horsepower classes 1–4 and the other for horsepower classes 5–8. This phenomenon was caused by the contrasting relationships of horsepower class (direct) and LPUE (inverse) to trawling depth (Table 7). Thus, larger

TABLE 7. Cumulative Option-2 effort (h), landings (t), and LPUE (kg/h), by depth interval and horsepower class, for rock sole from Two Peaks – Butterworth Ground, April–September 1960–81.

Depth interval (fathoms)	Horsepower class									
	1	2	3	4	5	6	7	8	9	Total[a]
					Effort (h)					
10–19	32	557	2365	2011	145	84	14	60	—	5 268
20–29	—	48	250	299	25	54	—	—	—	676
30–39	78	735	2947	1513	339	83	286	503	—	6 484
40–49	—	410	1200	592	206	792	433	1250	—	4 883
50–59	—	—	346	140	103	239	73	133	54	1 034
Total	110	1750	7108	4555	818	1252	806	1946	54	18 345
					Landings (t)					
10–19	17	623	1291	1307	25	49	7	15	—	3 424
20–29	—	5	60	217	4	22	—	—	—	308
30–39	9	288	1146	754	110	6	61	215	—	2 589
40–49	—	89	224	121	15	31	64	130	—	674
50–59	—	—	62	13	8	34	2	14	Tr[b]	135
Total	26	1005	2783	2502	162	142	134	374	Tr[b]	7 128
					LPUE (kg/h)					
10–19	520	1118	546	695	173	579	490	247	—	650
20–29	—	98	240	725	160	405	—	—	—	456
30–39	111	392	389	499	324	74	215	427	—	399
40–49	—	218	187	205	73	39	148	104	—	138
50–59	—	—	179	92	80	141	25	103	3	129
Total[c]	236	574	392	549	198	113	166	192	3	389

[a]Excluding class 9.
[b]Tr = trace (<0.5 t).
[c](Total Option-2 landings)/(total Option-2 effort).

horsepower classes did not expend much trawling effort in shallower water where LPUEs were high. This artifact probably explains the conclusion of Stocker and Fournier (1984) that "tonnage class was not a factor in fishing power directed at rock sole on this ground."

A data report (Foucher and Westrheim 1984) contains the details for Pacific cod, English sole, and rock sole from important grounds in Hecate Strait and for the species groups from areas 3C-N, 5A, 5B, 5C, and 5D.

Species Groups

In each area, the regression of $\overline{RFP}$ on horsepower class was reasonably linear. The R^2 values ranged from 0.67 (3C-N) to 0.89 (5D) (Table 8). Regression slopes were similar for areas 3C-N (0.125), 5A and 5B (0.120), and 5C (0.142), but only about half that for area 5D (0.271).

Regression slope was greater for area 5D (0.271), and as a result, $\overline{RFP}$ values were smaller for horsepower classes 1–3 (0.23–0.74 vs. 0.56–0.88) and larger for horsepower classes 5–10 (1.26–2.53 vs. 1.12–1.88). We believe that this disparity in RFP ratios among major areas is real and is caused by the topography of the trawling grounds. Our basis is anecdotal evidence provided by senior trawl captains. Essentially, in major areas where the actual trawling grounds are restricted in length and width, larger horsepower classes have little advantage over smaller ones. In area 5D, such spatial restraints are minimal.

To demonstrate the effect of standardizing effort, the RFPs for area 5D have been applied to the Canada–U.S. landing statistics for Pacific cod from Two Peaks – Butterworth Ground. To calculate the standardized effort the nominal effort in each trawl landing record is adjusted by the relative fishing power of the vessel making the landing (determined by its horsepower class, see Table 8).

Nominal (N) and standardized (S) effort exhibited the same trend throughout 1960–81: a gradual increase through 1974, and a substantial increase thereafter (Fig. 8). However, nominal effort exceeded standardized effort in each year during 1960–73, while the reverse occurred during 1974–81.

During 1960–73, N/S ratios were 1.13–1.92 and reflected the predominance of horsepower classes 2–4, while after 1973, there was an abrupt entry of horsepower classes 6–9 into the fleet (Tables 6 (landings) and 9). Thus the results of this effort-standardization exercise suggest that nominal effort probably overestimated "real" effort by 13–93% during 1960–73 and underestimated "real" effort by 8–37% during 1974–81. Trends in nominal and standardized LPUE were likewise similar, but nominal LPUE underestimated "real" LPUE during 1960–73 by 11-48% and overestimated "real" LPUE during 1974–81 by 9–57%.

Discussion

Vessel efficiency (RFP) for selected shelf species of Canadian trawlers is linearly related to horsepower class, but it is variable

TABLE 8. Estimated relative fishing power (RFP), by horsepower class, for Canadian trawlers landing selected shelf species[a] from areas 3C-N, 5A + 5B, 5C, and 5D, April–September 1960–81 (data in parentheses not included in computations).

Horsepower class	Area 3C-N (1960–81)			Area 5A + 5B (1965–81)			Area 5C (1960–81)			Area 5D (1960–81)		
	$\widehat{RFP}$	$\overline{RFP}$	N	$\widehat{RFP}$	$\overline{RFP}$	N	$\widehat{RFP}$	$\overline{RFP}$	N	$\widehat{RFP}$	$\overline{RFP}$	N
1	0.57	0.580	7	0.63	(0.753)	(7)	0.56	0.604	5	0.23	0.359	5
2	0.71	0.711	20	0.75	0.640	12	0.71	0.764	17	0.49	0.624	17
3	0.86	0.694	21	0.88	0.824	16	0.85	0.907	21	0.74	0.943	22
4	1.00	1.000	21	1.00	1.000	17	1.00	1.000	22	1.00	1.000	22
5	1.14	0.963	12	1.12	1.305	15	1.15	0.936	15	1.26	1.173	15
6	1.29	0.973	14	1.25	1.425	15	1.29	1.163	14	1.51	1.355	11
7	1.43	0.763	11	1.37	1.014	10	1.44	1.151	11	1.77	1.392	10
8	1.57	1.387	7	1.49	1.264	12	1.58	1.522	9	2.02	2.279	7
9	1.72	1.922	7	1.62	1.746	8	1.73	2.008	7	2.28	2.871	5
10	1.86	—	—	1.74	(3.760)	(5)	1.88	(1.504)	(2)	2.53	(0.725)	(1)
a		0.374			0.491			0.405			0.0226	
b		0.125			0.120			0.142			0.271	
R^2		0.67			0.69			0.84			0.88	
Cumulative landings (t)	20 904			12 648			24 275			34 375		

[a]3C-N, Pacific cod + lingcod + petrale sole; 5A + 5B, Pacific cod + lingcod + rock sole; 5C + 5D, Pacific cod + rock sole + English sole.

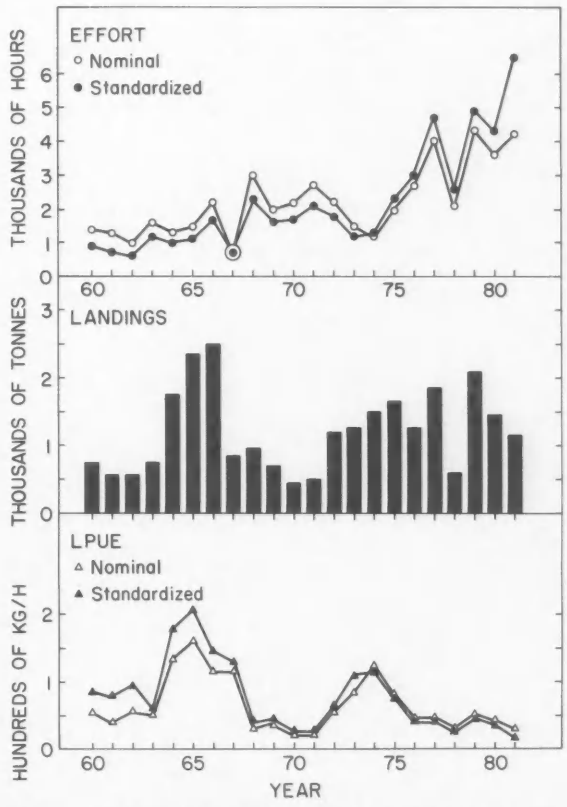

FIG. 8. Canada–U.S. landing statistics for Pacific cod from Two Peaks – Butterworth Ground, April–September 1960–81, using nominal and standardized effort.

TABLE 9. Landing statistics for Pacific cod from Two Peaks – Butterworth Ground, April–September 1960–81, using nominal (N) and standardized (S) effort.

Year	Effort (h)			Landings (t)	LPUE (kg/h)		
	N	S	N/S		N	S	N/S
1960	1374	901	1.52	744	541	827	0.65
1961	1322	686	1.93	543	411	792	0.52
1962	999	566	1.77	531	532	940	0.57
1963	1577	1212	1.30	755	479	624	0.77
1964	1292	1022	1.26	1773	1372	1735	0.79
1965	1462	1145	1.28	2368	1620	2068	0.78
1966	2177	1712	1.27	2492	1145	1456	0.79
1967	745	661	1.13	852	1144	1287	0.89
1968	2966	2327	1.27	946	319	407	0.78
1969	1966	1571	1.25	707	360	450	0.80
1970	2198	1669	1.32	430	196	258	0.76
1971	2669	2078	1.28	501	188	242	0.78
1972	2175	1778	1.22	1181	543	665	0.82
1973	1515	1158	1.31	1260	832	1088	0.76
1974	1215	1320	0.92	1519	1250	1152	1.09
1975	1988	2299	0.86	1672	841	727	1.16
1976	2651	3048	0.87	1233	465	405	1.15
1977	4029	4737	0.85	1858	461	392	1.18
1978	2094	2628	0.80	603	288	229	1.26
1979	4259	4855	0.88	2082	489	429	1.14
1980	3635	4296	0.85	1466	403	341	1.18
1981	4154	6549	0.63	1156	278	177	1.57

among species and trawling locations. Furthermore, RFP/horsepower class relationships are affected by extrinsic factors such as topography of trawling grounds and depth distribution of individual shelf species. There may well be other such factors as yet undiscovered. These results emphasize the need to carefully evaluate the results of any method of effort standardization.

In our opinion, the current study underestimates the increase

in "efficiency" of Canadian trawlers since 1960. Currently, unquantifiable factors such as LORAN C (1970s), LORAN C plotters (1980s), and vastly improved echo sounders have undoubtedly improved vessel efficiency. Hopefully, some quantification of these factors will be possible in the future.

We recognize that the accuracy of our current estimates of RFPs is limited. Important factors omitted in our analysis include trawl captain, quantified navigational aids, and possibly market conditions. Most of these would further increase the RFPs for trawlers operating in the 1970s and 1980s. The current, dynamic nature of the British Columbia groundfish industry requires that vessel efficiency be reevaluated regularly.

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Hormonal Growth Promotion and Evidence for a Size-Related Difference in Response to Estradiol-17β in Yellow Perch (*Perca flavescens*)[1]

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Malison, J. A., C. D. Best, T. B. Kayes, C. H. Amundson, and B. C. Wentworth. 1985. Hormonal growth promotion and evidence for a size-related difference in response to estradiol-17β in yellow perch (*Perca flavescens*). Can. J. Fish. Aquat. Sci. 42: 1627–1633.

Our studies indicate that estrogen(s) promote growth and may mediate sexually related dimorphic growth in yellow perch (*Perca flavescens*). (1) Neither 17α-methyltestosterone (MT) at 1.5–60 μg/g diet nor estradiol-17β (E_2) at 15–120 μg/g stimulated length or weight gain when fed for 85 d to age 0 perch that were initially 20–35 mm total length (TL) and 0.14–0.25 g total weight (TW). (2) In larger age 0 perch (initially 90–110 mm TL and 8–12 g TW), E_2 at 2 or 20 μg/g accelerated length and weight gain; MT, triiodothyronine, and zeranol failed to promote growth at all doses tested. (3) E_2 at 20 μg/g had differential effects when fed for 84 d to age 0 perch (initially 30–50 mm TL and 0.5–0.7 g TW) and age 1 perch (initially 90–110 mm TL and 8–12 g TW): E_2 stimulated weight gain in the larger fish within the first 28 d, but did not improve growth in the smaller perch until they reached 80–100 mm TL and 5–10 g TW (after day 56). These results demonstrate that E_2 promotes perch growth only after a certain size- or age-related maturational status has been reached. We suggest that this status is related to the onset of spermatogenesis, vitellogenesis, and sexually related dimorphic growth and may be linked to the maturation of hormone receptors.

Nos études révèlent que l'estrogène stimule la croissance et peut jouer un rôle dans la croissance liée au dimorphisme sexuel de la perchaude (*Perca flavescens*). (1) Ni 17α-méthyltestostérone (MT) à une concentration variant de 1,5 à 60 μg/g dans les aliments ou l'estradiol-17β (E_2) à une concentration allant de 15 à 120 μg/g n'ont stimulé un accroissement du poids ou de la longueur chez des perchaudes de 0 an nourries pendant 85 d et dont la longueur totale (LT) et le poids total (PT) initiaux variaient respectivement de 20 à 35 mm et de 0,14 à 0,25 g. (2) Chez les plus grosses perchaudes de 0 an (LT et PT initiaux : respectivement 90–110 mm et 8–12 g), E_2 à une concentration de 2 ou 20 μg/g a accéléré la croissance en longueur et en poids; le MT, la triiodothyronine et le zéranol n'ont pas stimulé la croissance à toutes les teneurs vérifiées. (3) Une concentration de 20 μg/g de E_2 avait une incidence différentielle quand elle était donnée pendant 84 d à des perchaudes de 0 an (LT et PT initiaux : respectivement 30–50 mm et 0,5–0,7 g) et de 1 an (LT et PT initiaux : respectivement 90–110 mm et 8–12 g) : E_2 a stimulé une augmentation du poids chez les plus gros poissons au cours des 28 premiers jours mais n'a pas amélioré la croissance chez les plus petites perchaudes avant qu'elles atteignent de 80 à 100 mm LT et de 5 à 10 g PT (après le 56e jour). Ces résultats prouvent que E_2 ne stimule la croissance de la perchaude qu'après un certain stade de maturation lié à la taille ou à l'âge. Les auteurs formulent l'hypothèse que ce stade est lié au début de la spermatogénèse, de la vitellogénèse et de la croissance liée au dimorphisme sexuel, et peut être en relation avec la maturation des récepteurs hormonaux.

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The influence of hormones on vertebrate growth has been studied for many years, and hormones and their analogs have long been used to promote growth in livestock (Borger et al. 1973; Heitzman 1974, 1978; Preston 1975; Heitzman et al. 1977). Recently, the potential of using such substances to improve growth in teleosts has been examined (see reviews by Yamazaki 1976; Donaldson et al. 1979; McBride et al. 1982). Much of this research has centered on a limited number of families, particularly the Salmonidae. To our knowledge, the effects of hormones on the growth of mesothermal "coolwater" fishes, such as the esocids and percids, have not been investigated.

Various hormones, including steroid and thyroid hormones, affect growth in both mammals (Daughaday 1981) and teleosts (Donaldson et al. 1979). Of the steroids, androgens have been used with the greatest success by investigators to promote growth in fish (Donaldson et al. 1979) and may have direct anabolic effects on vertebrate bone and muscle (Powers and Florini 1975; Wiedemann 1981). Estrogen and various compounds with estrogen-like activity, such as diethylstilbesterol and zeranol (a resorcylic acid lactone), improve growth in ruminants and certain other vertebrates (Borger et al. 1973;

[1]Presented in part at the Annual Meeting of the American Society of Zoologists, Louisville, KY, 27–30 December 1982 (Malison et al. 1983).

Heitzman et al. 1977; Wangsness et al. 1981). In teleosts, evidence to date for growth promotion by estrogens is rare (Donaldson et al. 1979). A possibility exists that exogenous estrogens may lower circulating thyroid hormone levels in some fish species (Olivereau et al. 1981). Thyroid hormones have wide-ranging effects on metabolism (Mosier 1981; Plisetskaya et al. 1983) and enhance growth in salmonids (Higgs et al. 1977).

In many economically important coolwater species, such as muskellunge (*Esox masquinongy*), walleye (*Stizostedion vitreum*), and yellow perch (*Perca flavescens*), females grow faster and reach a larger ultimate size than males (Scott and Crossman 1973; Schott et al. 1978; Schott 1980). Little is known about the physiology of sexual size dimorphism in teleosts (Peter 1979). This report deals with the effects of estradiol-17β (E_2),[2] 17α-methyltestosterone (MT),[2] triiodothyronine (T_3),[2] and zeranol (Z)[3] on the growth of the yellow perch as a representative coolwater fish. Experiments were designed to determine in perch (1) whether E_2, MT, T_3, or Z can be used to enhance growth and (2) to what extent androgens and estrogens influence sexually related dimorphic growth.

Materials and Methods

General Procedures

All fish used were the offspring of perch (captured from Lake Mendota, Madison, WI) that had been artificially spawned in the laboratory using the "dry" method outlined by Kayes (1978). Methods for intensively rearing larval perch have not yet been developed. Therefore, following incubation in the laboratory (8–10 d), eggs were relocated to fertilized ponds where the larvae hatched and were reared (Soderberg 1977). Perch were harvested, brought into the laboratory, and trained to accept a commercial diet (Silver Cup salmon feed, Murray Elevators, Murray, UT 84107) when they were about 20 mm total length (TL), the smallest size at which most fish (>80%) survive this transition (Best 1981). Prior to each experiment, fish were assigned and acclimatized to 110-L round fiberglass tanks (61.0-cm diameter × 50.5-cm depth, with 2-L/min flow) for 1 wk at environmental conditions optimum for perch culture (21 ± 1°C, 16-h light : 8-h dark photoperiod; see Huh et al. 1976). Fish were anesthetized with tricaine methanesulfonate (MS-222) for weighing and measuring.

All compounds tested were administered via the diet. For aquaculture, this method is probably the only cost-effective way to continuously treat large numbers of fish (Higgs et al. 1982). Experimental diets were prepared by mixing 100 g of feed with 100 mL of ethanol containing the appropriate hormone and evaporating off the alcohol in a 33°C oven or food dryer (Guerrero 1975). Fish were fed to satiation twice (experiment 1) or three times (experiments 2 and 3) daily. Diets were stored at 4°C between feedings.

Experiment 1

Age 0 yellow perch of 20–35 mm TL and 0.14–0.25 g total weight (TW) were randomly assigned to 30 experimental tanks at 30–35 fish per tank. Three tanks were assigned to each treatment group. Fish were fed one of 10 experimental diets containing the following: MT at 1.5, 15, 30, or 60 μg/g diet; E_2 at 15, 30, 60, or 120 μg/g diet; or cholesterol (C) at 0 or 120 μg/g diet (control diets). The treatment phase of the experiment lasted 85 d. Fish were then fed untreated diet for an additional 35 d. Length and weight measurements on individual fish were taken on days 0, 50, 85, and 120. Parameters calculated for the mean of the fish in each tank were TL, TW, specific growth rate (SGR), and condition factor (K), the latter as suggested by Carlander (1977):

$$\text{SGR} = \frac{\ln \text{final TW} - \ln \text{initial TW}}{\text{days}} \times 100$$

$$\text{K} = \frac{\text{TW}}{(\text{standard length})^3} \times 10^5$$

with TW in grams and standard length in millimetres. The data were examined to determine treatment and post-treatment effects by one-way analysis of variance (ANOVA) using appropriate preplanned orthogonal comparisons.

Experiment 2

Perch of 90–110 mm TL and 8–12 g TW (age 0) were randomly assigned to 36 experimental tanks and 18 treatments (two tanks per treatment) at 25 fish per tank. Based on our experience, this was the minimum number of perch of this size needed (under these conditions) to insure social interaction and social facilitation of feeding behavior. Twelve fish in each tank were fin-clipped for individual identification. (This was the maximum number of fish per tank that could be individually clipped without interfering with equilibrium or swimming ability.) Fish were fed one of 18 experimental diets: C at 20 μg/g diet as a control; MT, E_2, or Z at 0.2, 2, or 20 μg/g diet; T_3 at 2 or 20 μg/g diet; or a combination of E_2 plus T_3 at all the above doses. Test diets were administered for 76 d, and the TL and TW of each clipped fish were recorded on days 0, 28, 56, and 76. After the experiment, the clipped fish were autopsied to determine sex.

Gain in TL and TW, and condition factor of individual fish were examined by two-way (sex × treatment) ANOVA followed by Dunnett's *t* test (Steele and Torrie 1960). Although there were 24 clipped fish per treatment, some treatment groups had only eight fish of one sex. Because Dunnett's *t* test requires a balanced design (an equal number of observations per data subset), the data from only eight (randomly selected where necessary) fish per sex of each treatment group were analyzed. The data for each treatment were pooled across tanks because differences between tanks within treatments were not significant.

Experiment 3

Age 0 perch of 30–50 mm TL and 0.5–0.7 g TW were randomly distributed among 16 tanks at 65–70 fish per tank; age 1 perch of 90–110 mm TL and 8–12 g TW were distributed among 16 additional tanks at 25 fish per tank. The fish in each size group were fed one of four diets (four tanks per diet): C at 50 μg/g diet as a control, or E_2 at 2, 20, or 50 μg/g diet. The fish in each tank were counted and weighed collectively on days 0, 28, 56, and 84 of treatment. Mean gain in TW was examined for each size group by ANOVA and appropriate preplanned orthogonal comparisons.

[2]Sigma Chemical Company, St. Louis, MO 63178.

[3]6-(6,10-Dihydroxyundecyl)-β-resorcyclic acid-μ-lactone, Commercial Solvents Corporation, Terre Haute, IN 47808.

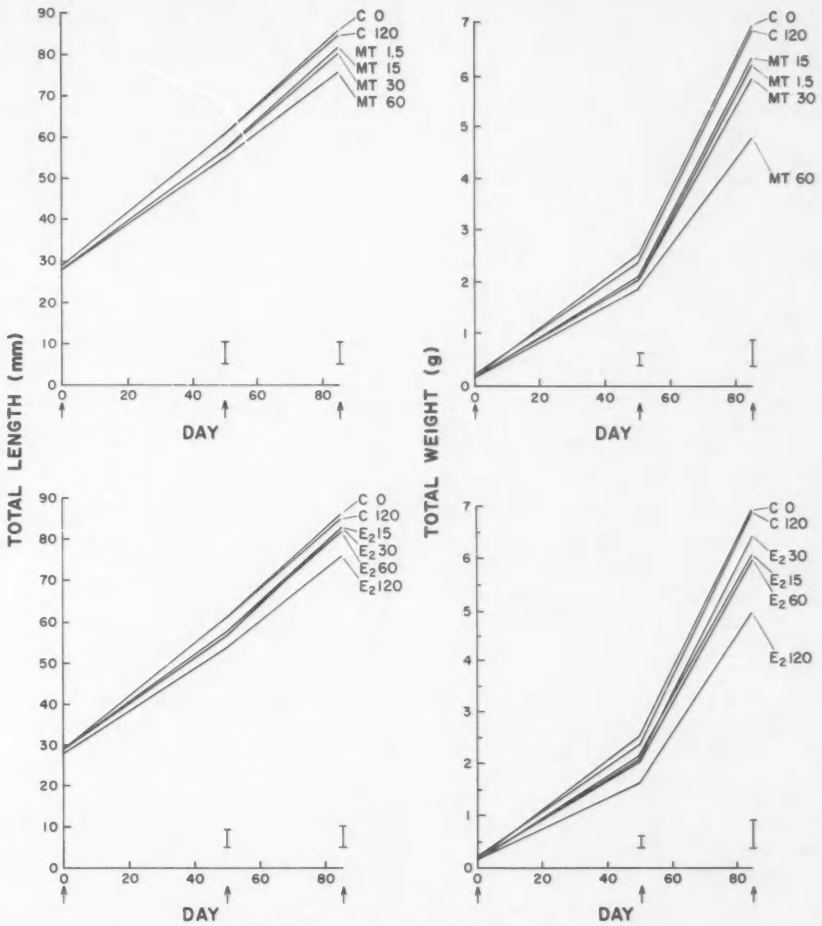

FIG. 1. Growth of yellow perch (initially 20–35 mm total length and 0.14–0.25 g total weight) treated with estradiol-17β (E_2), 17α-methyltestosterone (MT), or cholesterol (C) as a control. Dosages are shown in μg/g diet. Each point on days 0, 50, and 85 (indicated by arrows) represents the mean total length or total weight of the fish from three tanks with 30–35 fish per tank. Vertical bars depict the mean of standard errors for all treatments on days 50 and 85. Orthogonal contrasts for both length and weight data on day 85 revealed the following differences ($P < 0.01$) between treatment groups: C0 and C120 > (MT1.5 and MT15 > MT30 and MT60); C0 and C120 > ($E_2$15 and $E_2$30 > $E_2$60 and $E_2$120).

Results

Experiment 1

Yellow perch (initially 20–35 mm TL and 0.14–0.25 g TW) fed either MT or E_2 grew slower ($P < 0.01$) than both (cholesterol) control groups during the treatment phase of the experiment (Fig. 1). Growth impairment by both MT and E_2 was proportional to dose. The condition factor of hormone-treated fish did not differ statistically from controls, indicating that growth responses were similar for both length and weight. During the post-treatment phase of the experiment, the specific growth rate of E_2-treated perch was significantly greater than that of controls, while growth rates of MT-treated fish and controls did not differ (Table 1).

Experiment 2

In yellow perch that were initially 90–110 mm TL and 8–12 g TW, E_2 at 2 and 20 μg/g diet improved length and weight gain when administered either alone or together with T_3 at 2 μg/g diet (Table 2). At 20 μg/g diet, T_3 countered the growth-promoting effect of E_2. No other hormonal treatments had a significant effect on growth, and none of the treatments influenced condition factor. Estradiol-17β stimulated the growth of both male and female perch (Table 3). For day 0, ANOVA revealed no differences between the sexes in length or weight (Table 4). During the experiment, females collectively outgrew males in length by day 28 and in weight by day 56 (both $P < 0.05$). This trend continued through day 76 ($P < 0.01$), by which time females also had a greater condition factor ($P < 0.05$) than

TABLE 1. Specific growth rates (SGR = (ln final weight − ln initial weight)·days^{-1}·100) of yellow perch for a 35-d period following 85 d of steroid treatment. Data represent $\bar{x} \pm$ SE; $N = 3$ replicate groups of fish per treatment.[a]

Dose (μg/g diet)	Cholesterol	17α-Methyltestosterone	Estradiol-17β
0	1.99±0.05	—	—
1.5	—	1.97±0.03	—
15	—	1.87±0.04	1.97±0.08[b]
30	—	1.96±0.07	2.12±0.06[b]
60	—	2.02±0.05	2.11±0.04[b]
120	1.89±0.06	—	2.17±0.07[b]

[a]Perch at the beginning and end of treatment (beginning of post-treatment period) were 20–35 mm total length (TL) and 0.14–0.25 g total weight (TW) and 70–90 mm TL and 4.5–7.0 g TW, respectively.

[b]Orthogonal contrasts revealed that specific growth rates of fish treated with estradiol-17β (all doses) were greater than those treated with both doses of cholesterol ($P < 0.05$).

males. At no time did ANOVA indicate any significant interaction between treatment and sex, and inspection of means revealed no obvious sex-related differences between experimental treatments.

Experiment 3

Yellow perch initially 90–110 mm TL and 8–12 g TW that were treated with E_2 at 20 μg/g diet gained more weight than controls within the first 28 d ($P < 0.05$) and throughout the remainder of the experiment (Fig. 2). However, in smaller perch that were initially 50–70 mm TL and 0.5–0.7 g TW, E_2 did not significantly improve weight gain until after day 56, at which time these fish were 80–100 mm TL and 5–10 g TW. Estradiol-17β at 50 μg/g diet depressed weight gain in both size groups of fish.

Discussion

Our results indicate that estrogens promote growth and may play a role in mediating sexually related dimorphic growth in yellow perch. The fact that E_2 stimulated growth and an androgen had either negligible (at low doses) or negative (at high doses) effects in this species contrasts with the findings on most other teleosts (Donaldson et al. 1979), and demonstrates that species-related differences in the effect of steroids on growth occur in teleosts, just as in mammals (Heitzman 1978). Triiodothyronine had no positive influence on perch growth when administered alone or with E_2 (Table 2). In most fishes studied to date, normal thyroid function is essential to normal growth (Donaldson et al. 1979). Collectively, our results suggest that exogenous E_2 at the levels used does not suppress thyroid function in perch, as it does in the eel, *Anguilla anguilla* (Olivereau et al. 1981).

Estradiol-17β enhanced the growth of both sexes of perch but did not eliminate the normal pattern of sex-related dimorphic growth when treatment was initiated in fish that were 90–110 mm TL and 8–12 g TW (Table 3). In other studies (unpublished), we have found that E_2 treatment of male perch initially 90–110 mm TL and 8–12 g TW does not result in sex reversal. These findings indicate that the influence E_2 has on the growth of perch is not simply the result of a feminizing effect on males, as

TABLE 2. Growth of yellow perch (initially 90–110 mm total length and 8–12 g total weight) treated with estradiol-17β (E_2), 17α-methyltestosterone (MT), triiodothyronine (T_3), zeranol (Z), cholesterol (C), or combinations of E_2 and T_3. Data represent $\bar{x} \pm$ SE; $N = 16$ fish (8 of each sex).

Hormone	Dose (μg/g diet)	76-d length gain (mm)	76-d weight gain (g)	Day 76 condition factor
C	20.0	44.9±1.6	24.31±2.42	1.89±0.03
MT	0.2	48.1±1.9	28.23±2.18	1.91±0.03
MT	2.0	49.5±1.5	28.87±1.92	1.90±0.02
MT	20.0	49.1±1.3	27.43±1.57	1.84±0.02
Z	0.2	46.6±1.5	25.71±1.02	1.90±0.02
Z	2.0	50.6±1.5	31.39±1.80	1.94±0.03
Z	20.0	48.1±1.3	26.81±1.17	1.95±0.03
T_3	2.0	47.8±1.6	28.85±1.65	1.97±0.04
T_3	20.0	43.4±2.0	22.13±1.78	1.84±0.03
E_2	0.2	47.2±2.5	28.77±2.92	1.93±0.03
E_2	2.0	54.9±1.8[a]	34.86±1.40[a]	1.91±0.03
E_2	20.0	53.8±1.7[a]	40.65±2.27[a]	2.01±0.03
T_3 2.0 / E_2 0.2		45.4±1.7	24.75±1.92	1.87±0.03
T_3 2.0 / E_2 2.0		55.2±2.1[a]	33.49±2.74[a]	1.93±0.03
T_3 2.0 / E_2 20.0		52.8±1.6[a]	35.03±2.12[a]	1.99±0.02
T_3 20.0 / E_2 0.2		49.2±1.8	28.16±1.43	1.92±0.03
T_3 20.0 / E_2 2.0		51.6±2.2	28.60±2.07	1.84±0.03
T_3 20.0 / E_2 20.0		48.6±1.3	28.78±2.08	1.92±0.04

[a]Mean different than that for C ($P < 0.05$, Dunnett's t test).

Donaldson et al. (1979) suggested was the case in guppies (*Poecilia reticulata*) and platyfish (*Platypoecilus maculatus*).

However, the possibility that feminizing male perch may increase their growth rate cannot be excluded. In experiment 1, E_2 did not stimulate the growth of perch smaller than 80–100 mm TL and 7–10 g TW during treatment (Fig. 1). But following treatment, the same E_2-treated fish (as a group) outgrew controls (Table 1). In a separate study, we demonstrated that E_2 treatment of males initially 20–35 mm TL and 0.14–0.25 g TW resulted in sex inversion (Malison et al. 1986). Taken together, these findings suggest that the greater growth rate observed in smaller perch after termination of E_2 treatment was due to feminized males outgrowing normal males. This hypothesis could not be verified in experiment 1 because growth rates of individual (male and female) fish were not examined.

Cumulatively, our experimental results indicate that yellow perch must reach a size (or age) threshold before exogenous E_2 has a positive influence on growth. This occurs in perch at 80–100 mm TL and 5–10 g TW, the same size at which females normally begin to outgrow males (Schott et al. 1978). Schott (1980) suggested that body size, rather than chronological age

TABLE 3. Comparison of growth of male and female yellow perch treated with estradiol-17β (E_2). Data represent $\bar{x} \pm$ SE; $N = 8$ fish.[a]

Hormone and dose (μg/g diet)		76-d length gain[b]		76-d weight gain[b]	
		Male	Female	Male	Female
C	20	43.29±2.22	46.56±2.35	23.89±2.84	24.73±3.83
E_2	2	49.85±1.75	59.33±4.10	33.13±1.63	36.57±2.20
E_2	20	48.86±1.72	58.63±1.60	35.16±2.41	46.13±2.83
T_3 E_2	2 2	51.33±2.90	59.00±2.31	30.74±4.53	36.18±2.21
T_3 E_2	2 20	50.63±2.07	55.00±2.31	33.51±2.59	36.55±3.56

[a]Cholesterol (C) was included in the diet fed to controls. Triiodothyronine (T_3) at the dose shown had no effect on the response of fish to E_2.
[b]Perch treated with E_2 or T_3 and E_2 at the levels indicated had greater 76-d length and weight gains than C-treated controls ($P < 0.05$).

TABLE 4. Growth of male vs. female yellow perch, with data pooled across hormonal treatments. Data represent $\bar{x} \pm$ SE; $N = 144$ fish pooled across all treatments in experiment 2 (see Table 2).

Parameter[a]	Male	Female
Day 0 total length (mm)	102.19±0.62	101.46±0.70
28-d length gain (mm)*	23.20±0.41	24.95±0.37
56-d length gain (mm)**	38.20±0.50	42.59±0.45
76-d length gain (mm)**	46.21±0.57	52.28±0.55
Day 0 total weight (g)	11.07±0.21	10.71±0.23
28-d weight gain (g)	11.22±0.21	11.87±0.22
56-d weight gain (g)*	20.03±0.46	22.60±0.51
76-d weight gain (g)**	26.01±0.61	30.98±0.72
Day 0 condition factor	1.75±0.01	1.73±0.01
Day 28 condition factor	1.89±0.01	1.89±0.01
Day 56 condition factor	1.88±0.01	1.89±0.01
Day 76 condition factor*	1.89±0.01	1.94±0.01

[a]ANOVA indicated females > males at $*P < 0.05$ or $**P < 0.01$ but no treatment × sex interactions.

or environmental cues, is the primary factor dictating the onset of sexually related dimorphic growth in perch. Likewise, size may be more important than age in determining the growth response of perch to E_2. The hypothesis that attaining a certain body size is critical to the onset of certain physiological events is not without precedent. For example, body size and the initiation of sexual maturation are closely linked in some mammalian species (Foster and Ryan 1981). In addition, Zucker (1972) suggested that the attainment of a minimum body weight is more important than chronological age in determining when estradiol first influences the feeding behavior of rats.

Sex-related growth dimorphism in perch could be the result of several factors (e.g. genetic, behavioral, or physiological), including differences in competition, food consumption, or conversion efficiency. Regardless of cause, the likelihood is that such sex-related differences are mediated by the endocrine system. In most mammals, sexually related dimorphic growth (with males generally outgrowing females) begins at puberty. One widely accepted theory is that these growth differences result, either directly or indirectly, from changes in steroid hormone (specifically, estrogen and testosterone) levels ob-

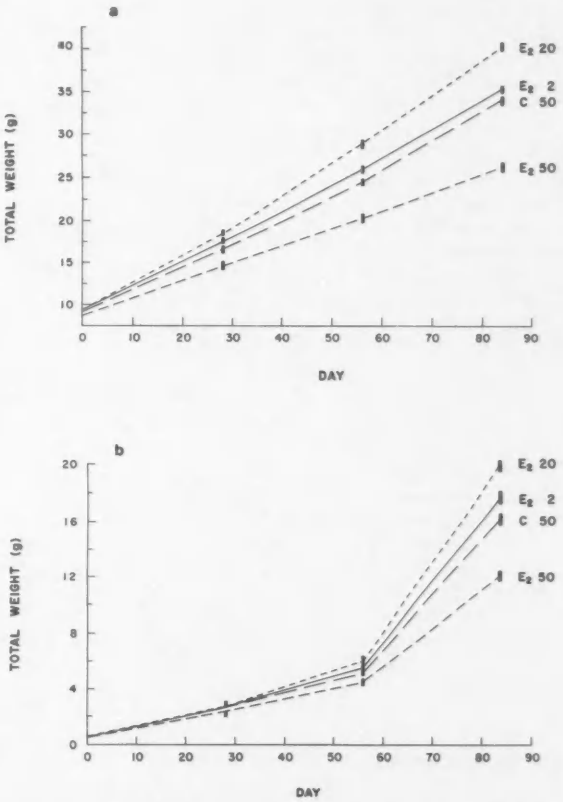

FIG. 2. Effect of estradiol-17β (E_2) vs. cholesterol (C) on weight gain of yellow perch that were initially (a) 90–110 mm total length and 8–12 g total weight or (b) 30–50 mm total length and 0.5–0.7 g total weight. Dosages are shown in μg/g diet. Each bar represents the mean ± SE of the fish from four tanks, with (a) 25 or (b) 65–70 fish per tank. Orthogonal contrasts revealed the following differences in weight gain. (a) Day 28: ($E_2$20 > $E_2$2 and C50) > $E_2$50, $P < 0.05$; days 56 and 84: ($E_2$20 > $E_2$2 and C50) > $E_2$50, $P < 0.01$. (b) Day 56: $E_2$20, $E_2$2, and C50 > $E_2$50, $P < 0.05$; day 84: ($E_2$20 > $E_2$2 and C50) > $E_2$50, $P < 0.01$.

served during puberty (Daughaday 1981). The fact that female perch normally begin to outgrow males at the same size at which exogenous E_2 begins to promote growth suggests that sexually related dimorphic growth in perch may be mediated by the endocrine system, just as in mammals. Further support for this idea comes from the fact that two other steroid-dependent processes, spermatogenesis and vitellogenesis, are first observed in perch when they reach this same size (Malison et al. 1986). The onset of gonadal recrudescence in certain female salmonids has been associated with increasing serum levels of E_2 (Billard et al. 1978). If similar hormonal changes occur coincident with gonadal maturation in perch, then elevated E_2 levels could be (partially or entirely) responsible for the onset of sexually related dimorphic growth.

The mechanism of action of estrogens in promoting perch growth is unknown. Estrogens fail to stimulate overall body growth in most vertebrates and are not generally considered to have direct anabolic effects on muscle or bone (Daughaday 1981). However, estrogens do promote overall body growth in ruminants, probably by stimulating the release of growth hormone, somatomedins, or insulin (Hafs et al. 1971; Preston 1975; Wiedemann 1981). In rodents, estrogens exert a negative influence on food consumption, apparently by affecting appetite control centers in the hypothalamus (Bray 1974) and altering lipid metabolism (Wade and Gray 1979). In fish (depending on species), either estrogens or androgens can have a positive effect on food consumption (Peter 1979). Considering the above, it seems likely that E_2 promotes perch growth indirectly — through either the endocrine system, the central nervous system, or changes in metabolism — rather than through a direct anabolic effect on muscle and bone.

The reason for a lack of a growth-promoting effect by E_2 in small (<80 mm TL) perch is unclear. One prerequisite for a hormone to exert an effect is that receptor sites must be present in target tissues. Receptor development seems to be the crucial step in the maturation of several vertebrate endocrine systems (Presl et al. 1970; Odell and Swerdloff 1975; May and Knowland 1981; Slabaugh et al. 1982). In *Xenopus laevis*, May and Knowland (1981) demonstrated that exogenous estrogen can induce an increase in hepatic estrogen receptors (necessary for estrogen-induced vitellogenin synthesis), but only after a precise maturational stage is reached. Perhaps a similar system is present in yellow perch, in which those estrogen receptors involved in mediating growth develop only after a specific maturational status (equivalent to 80–100 mm TL and 5–10 g TW body size) is achieved. Regardless of mechanism, our results demonstrate that E_2 promotes growth and may have a functional role in mediating the growth of perch once they reach a critical size.

Acknowledgments

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Comparison of Summer and Winter Oxygen Consumption Rates in a Temperate Dimictic Lake

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Linsey, G. A., and D. C. Lasenby. 1985. Comparison of summer and winter oxygen consumption rates in a temperate dimictic lake. Can. J. Fish. Aquat. Sci. 42: 1634–1639.

In a temperate dimictic lake in southern Ontario, the winter rate of oxygen loss determined from oxygen profiles differed considerably from the summer hypolimnetic rate, although the sediment oxygen demand (SOD) and water column oxygen demand (WOD) did not change significantly (SOD: winter = 0.018 mg $O_2 \cdot L^{-1} \cdot d^{-1}$, summer = 0.020 mg $O_2 \cdot L^{-1} \cdot d^{-1}$; WOD: winter = 0.032 mg $O_2 \cdot L^{-1} \cdot d^{-1}$, summer = 0.027 mg $O_2 \cdot L^{-1} \cdot d^{-1}$). In summer, the sum of SOD and WOD (0.047 mg $O_2 \cdot L^{-1} \cdot d^{-1}$) closely approximated the hypolimnetic deficit (0.040 mg $O_2 \cdot L^{-1} \cdot d^{-1}$), but in winter, SOD plus WOD (0.050 mg $O_2 \cdot L^{-1} \cdot d^{-1}$) greatly overestimated the observed consumption rate (0.003 mg $O_2 \cdot L^{-1} \cdot d^{-1}$). Measurement of primary production and an estimate of rainwater influx revealed that both could be significant sources of oxygen input during winter. Although both WOD and SOD were found to vary significantly between 10 sampling sites, a central station yielded seasonal mean values that closely approximated those obtained from combining the data from all stations.

Dans un lac dimictique tempéré du sud de l'Ontario, le taux d'épuisement de l'oxygène en hiver déterminé à l'aide de profils de la teneur en oxygène est nettement différent du taux observé dans l'hypolimnion en été quoique la demande d'oxygène du sédiment (SOD) et de la colonne d'eau (WOD) n'ont pas varié de façon significative (SOD : hiver = 0,018 mg $\cdot L^{-1} \cdot d^{-1}$ O_2, été = 0,020 mg $\cdot L^{-1} \cdot d^{-1}$ O_2; WOD : hiver = 0,032 mg $\cdot L^{-1} \cdot d^{-1}$ O_2, été = 0,027 mg $\cdot L^{-1} \cdot d^{-1}$ O_2). En été, la somme du SOD et du WOD (0,047 mg $\cdot L^{-1} \cdot d^{-1}$ O_2) s'approche étroitement du déficit hypolimnétique (0,040 mg $\cdot L^{-1} \cdot d^{-1}$ O_2) mais en hiver, cette valeur (0,050 mg $\cdot L^{-1} \cdot d^{-1}$ O_2) surestime beaucoup le taux de consommation observé (0,003 mg $\cdot L^{-1} \cdot d^{-1}$ O_2). La quantification de la production primaire et une estimation de l'apport en eau de pluie révèlent qu'elles peuvent être des sources importantes d'apport d'oxygène en hiver. Quoique le WOD et le SOD variaient nettement à 10 stations d'échantillonnage, des valeurs moyennes saisonnières qui s'approchaient étroitement de celles obtenues par cumul des données recueillies à toutes les stations ont été observées à une station centrale.

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Recent work concerned with dissolved oxygen in lakes has been directed towards the development of empirical models designed to predict hypolimnetic and winter oxygen depletion rates using such parameters as phosphorus retention (Cornett and Rigler 1979), mean depth (Welch et al. 1976; Barica and Mathias 1979), the initial oxygen storage (Jackson 1979), or a combination of morphometry and temperature (Charlton 1980). In these models, the lake oxygen depletion rates are estimated by determining changes in depth profiles of oxygen concentration with time. This procedure provides little insight into the components consuming oxygen. The processes contributing to oxygen consumption in lakes can be divided into the two general compartments of sediment oxygen demand (SOD) and water column oxygen demand (WOD) (Hutchinson 1957). In the few attempts that have been made to determine the relative contribution of each compartment, usually only the SOD has actually been quantified (Lund et al. 1963; Hargrave 1972; Lasenby 1975; Barica and Mathias 1979; Mathias and Barica 1980). The difference between SOD and the total lake oxygen loss determined from profiles was assumed to be the result of oxygen loss in the water column (WOD). Evidence from other studies, however, suggests that this assumption may be incorrect. Welch et al. (1976) concluded that in the small lakes in their study, slushing events, inflow, and outflow may have altered the winter oxygen depletion rates. Cornett and Rigler (1980) suggested that in summer, the additions of oxygen to the hypolimnion by photosynthesis or vertical turbulence may alter the depletion rate.

If the depletion rate, as measured by changes in oxygen profiles with time, is to be related to other parameters, quantitative estimates of additions and losses of oxygen to the lake under ice in winter and the hypolimnion in summer must be made to improve the accuracy and precision of the relationships. Our study compared the oxygen depletion rate as measured by summing SOD and WOD with the oxygen depletion rate determined from changes in oxygen profiles with time. As well, we compared the lake oxygen depletion rate (from profiles), SOD, and WOD, measured at a single station located at the

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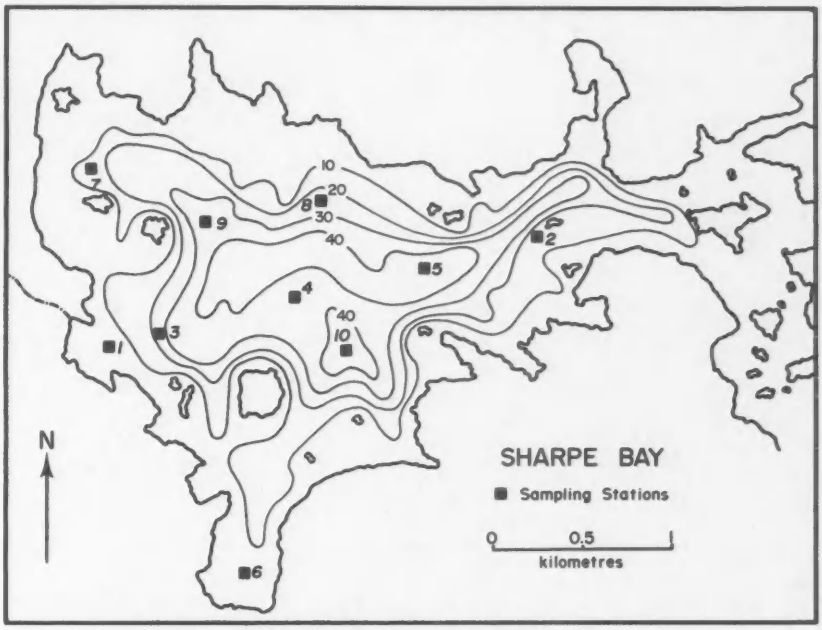

FIG. 1. Bathymetric detail and locations of 10 sampling stations in Sharpe Bay.

point of maximum lake depth, with the corresponding values obtained from multiple sampling sites.

Methods

This study was carried out in an isolated basin (Sharpe Bay) of Jack Lake located in southern Ontario (44°40′N, 78°02′W). Sharpe Bay has a surface area of 530 ha with mean and maximum depths of 16.1 and 43 m, respectively, and a catchment area of 2229 ha. Outflow from Sharpe Bay passes through a narrow, shallow channel connecting it with the other lake basins.

All dissolved oxygen determinations were performed using the azide modification of the Winkler titrimetric method (American Public Health Association 1976) with 0.05 mol·L^{-1} sodium thiosulphate dispensed from a 2.5-mL micrometer buret.

Water samples for oxygen profiles were obtained using a parastaltic pump from depths of 0, 1, 5, and subsequent 10-m intervals at 10 sites in Sharpe Bay. During summer, the 0 m depth was replaced by samples taken at the thermocline.

The 10 sampling sites were chosen to provide duplicate SOD data for sediments located at depths of 5, 15, 25, 35, and 43 m with the greatest possible horizontal separation between sites of equal depth (Fig. 1). Biweekly SOD determinations were made at all 10 sites during winter and were continued for a single site at each depth in summer. On each sampling date, three sediment cores were obtained at each site using a K.B. corer (Brinkhurst et al. 1969) and Plexiglas cores 50 cm in length having inside diameters of 5 cm. Each tube was fitted with a matched "O" ring-sealed Plexiglas piston containing a valved sampling port. A small magnetic stirring propeller suspended on the underside could be rotated by induction from a magnet externally mounted on an electric motor (see Jackson 1979 for a detailed diagram). After coring, each tube contained 15–25 cm of sediment with 25–35 cm of the overlying water column. Great caution was taken to minimize the disturbance to the sediment–water interface. The bottoms of the tubes were sealed with rubber stoppers and the pistons inserted into the upper ends, expelling all air bubbles through the sampling port. These cores were transported to the laboratory in insulated containers. Within a few hours, the cores were placed into dark incubators at in situ temperatures for a period of 8 h. Before and after the incubation period, the water in the cores was gently stirred to insure a homogeneous distribution of dissolved oxygen without disturbing the sediments. Aliquots of 150 mL were then extracted from the overlying water into glass-stoppered bottles by depressing the piston, and the concentrations of dissolved oxygen measured.

The oxygen loss that occurred in the water column within the core tubes was extrapolated from the WOD values obtained from the deepest sample taken at the corresponding station and subtracted from the total oxygen loss in the cores. The remainder was attributed to uptake by the sediments. This correction was always found to be less than 5% of the SOD.

WOD profiles were determined at each station on each sampling date. Water samples were obtained from the same depths as those used to measure dissolved oxygen profiles. From each depth, three 300-mL glass-stoppered BOD bottles were filled and sealed with plastic caps designed to prevent the evaporation of the water seals during incubation. All bottles and stoppers were autoclaved prior to each WOD determination. One of the triplicate bottles from each depth was randomly selected and its oxygen concentration determined. This value was used as the initial oxygen concentration for WOD calculations at that depth. The remaining two bottles were incubated in the dark at in situ temperatures for 48 h. After incubation, oxygen concentrations were determined yielding duplicate estimates of the final oxygen concentrations for each depth. The mean of these results was used to calculate the WOD rate (milligrams O_2 per litre per day).

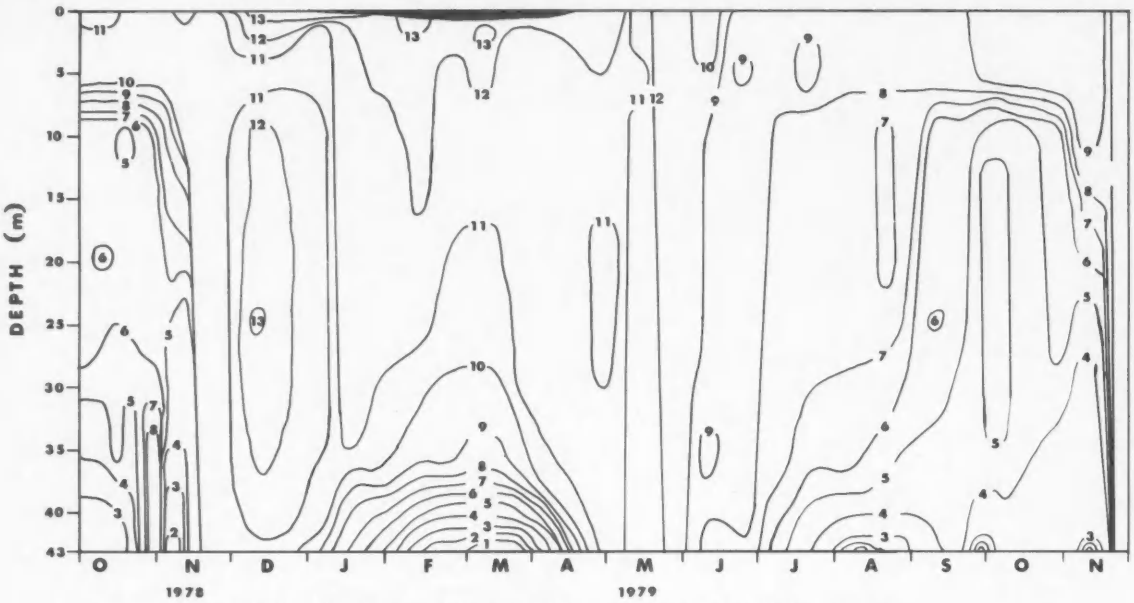

FIG. 2. Dissolved oxygen isopleths at the central station (station 5) in Sharpe Bay.

Approximately monthly throughout the 1-yr period of our study, phytoplankton production rates were measured using the ^{14}C tracer technique with in situ incubations. During winter, one dark and two light bottles were incubated at depths of 0, 0.5, 1, 2, 4, 5, 8, and 10 m with 12, 15, and 30 m being added when ice was absent. When incubations were carried out under ice cover, the bottles were suspended 1–2 m away from the auger hole, and care was taken to eliminate any light from entering the water column through the hole. Incident solar radiation was continuously monitored to allow the calculation of daily carbon assimilation rates. A photosynthetic quotient of 1.2 was used to estimate oxygen production rates from carbon uptake (Wetzel and Likens 1979).

Results

Fall turnover in Sharpe Bay began in mid-November and the water cooled to temperatures below 3°C for the duration of the winter. Thermal stratification was again apparent by mid-July.

Dissolved oxygen profiles revealed that although concentrations at 43 m were less that 1 $mg \cdot L^{-1}$ in late summer and winter, anoxic conditions did not occur (Fig. 2). Little horizontal variation in concentration was noted at any depth, the coefficients of variation for any site on a particular sampling date usually being less than 5% and never exceeding 10%. No significant difference ($P < 0.05$) was found to exist between the seasonal mean oxygen concentrations measured at the central, deep sampling site (station 5, Fig. 1) and the corresponding values calculated from the means of concentrations obtained from all 10 stations.

To evaluate the rates of oxygen depletion or the oxygen deficit, the volume-weighted oxygen concentrations calculated from oxygen profiles were regressed against time for the whole lake during winter and the hypolimnion in summer (Table 1). The calculated winter whole lake deficit was 0.003 mg $O_2 \cdot L^{-1} \cdot d^{-1}$ and the summer hypolimnetic deficit was 0.040 mg $O_2 \cdot L^{-1} \cdot d^{-1}$.

In the water column, under winter ice cover, oxygen consumption was comparatively low, with highest rates occurring adjacent to the ice–water and the sediment–water interfaces (Fig. 3). This distribution was observed regularly at all stations, but the higher near-sediment rates diminished at the shallower depths. This pattern persisted until the end of May when greater WOD was noted throughout the water column. Beginning in June, when thermal stratification became stable, WOD became consistently higher in the epilimnetic water, with peak rates occurring in samples taken at the thermocline. Immediately below this and in the upper strata of the hypolimnion, WOD decreased, but high rates again became apparent below 35 m.

Significant horizontal variation in WOD was found to occur at all depths (ANOVA, $P < 0.05$). To determine at which depths the magnitude of this variation was greatest, the coefficients of variation were calculated for each stratum, and as may be expected, less horizontal variation was found to occur in the summer epilimnion as a result of wind-induced mixing.

Mean seasonal volume-weighted WOD was calculated for the whole lake in winter and the volume below 10 m in summer, using both the data collected at the central site (station 5) and values calculated from the mean of all stations. Values calcu-

TABLE 1. Seasonal volumetric rates of oxygen depletion determined by regression analysis for data from the central station (5) and data calculated from mean oxygen concentration from all stations.

	Oxygen loss ($mg \cdot L^{-1} \cdot d^{-1}$)	r	n
Winter, whole lake			
Station 5	0.003	−0.28	7
All stations	0.003	−0.42	11
Summer, below 10 m (hypolimnion)			
Station 5	0.041	−0.99	13
All stations	0.040	−0.98	13

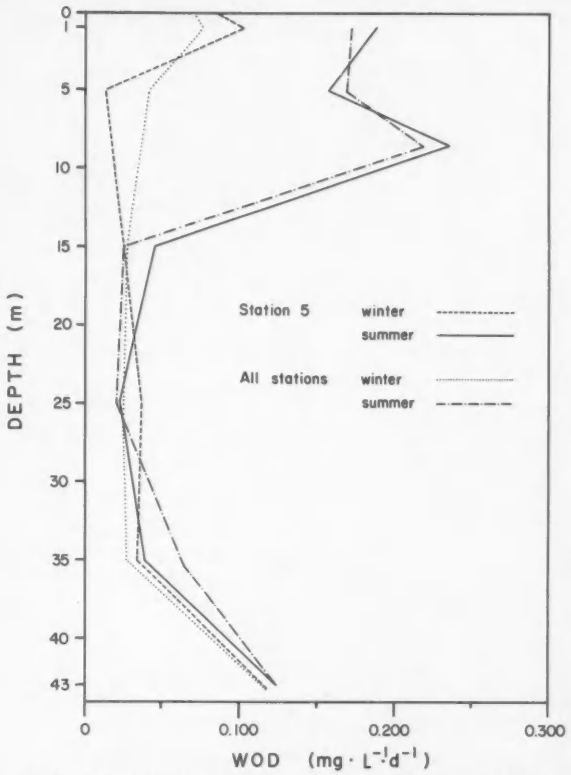

FIG. 3. Depth distribution of seasonal mean WOD values showing close agreement between values obtained at station 5 and those calculated from means of all stations in Sharpe Bay.

lated from WOD profiles measured at the central site (station 5) did not differ significantly from those calculated using data from all of the stations ($P < 0.005$). This was true for both the winter whole-lake values and the summer hypolimnion WOD (Table 2).

Comparisons of SOD at stations of equal depth sampled during winter showed no significant differences ($P < 0.05$) between sites. A multiple-comparison ANOVA (Scheffe's procedure) was used to examine the seasonal mean SOD at all measured depths. During winter, the highest SOD occurred at the 15-m sediments (0.041 mg $O_2 \cdot cm^{-2} \cdot d^{-1}$), this value being significantly higher than those measured at 5 and 43 m (0.024 and 0.025 mg $O_2 \cdot cm^{-2} \cdot d^{-1}$, respectively, Table 3). In summer,

TABLE 2. Seasonal mean (±1 SD) volume-weighted WOD for data obtained from the central station (5) and the means from all stations in Sharpe Bay.

	WOD (mg $O_2 \cdot L^{-1} \cdot d^{-1}$)
Winter, whole lake	
Station 5	0.024±0.015
All stations	0.032±0.022
Summer, below 10 m (hypolimnion)	
Station 5	0.026±0.016
All stations	0.027±0.016

TABLE 3. Mean (±1 SD) summer and winter SOD rates for sediments at five depths in Sharpe Bay.

Depth (m)	Summer SOD (mg $O_2 \cdot cm^{-2} \cdot d^{-1}$)	Winter SOD (mg $O_2 \cdot cm^{-2} \cdot d^{-1}$)
5	0.051±0.018	0.024±0.016
15	0.032±0.013	0.041±0.028
25	0.036±0.014	0.031±0.008
35	0.039±0.020	0.027±0.023
43	0.026±0.022	0.025±0.022

the maximum SOD occurred at 5 m (0.051 mg $O_2 \cdot cm^{-2} \cdot d^{-1}$), a value significantly higher than the 43-m SOD (0.026 mg $O_2 \cdot cm^{-2} \cdot d^{-1}$). A comparison of winter and summer SOD at each depth indicated that significantly higher values occurred in summer at only the 5- and 35-m sediments.

To allow an oxygen budget to be constructed, whole-lake SOD was calculated by weighting data from each depth by the sediment area occurring in the strata that they represented. For example, SOD measured at 5 m was multiplied by the sediment surface area between 0 and 10 m. The sum of these was then divided by the total lake volume to provide volume-weighted SOD rates. This calculation was done for the whole lake during winter and for the hypolimnion below 10 m during summer. Figure 4 illustrates the consistent, relatively similar nature of the volume-weighted SOD throughout most of the year. During winter, whole-lake SOD and that below 10 m are very similar. In summer, the whole-lake rates are higher than those exhibited by the hypolimnetic sediments as a result of increased oxygen uptake by the littoral (5 m) sediments.

Primary production measurements revealed that even though only a small portion of the total annual carbon assimilation occurred under ice and in the hypolimnion (Fig. 5), it provided 0.022 mg $O_2 \cdot L^{-1} \cdot d^{-1}$ to the lake during winter and 0.011 mg $O_2 \cdot L^{-1} \cdot d^{-1}$ to the hypolimnion in summer.

A significant input of oxygen to the surface waters of the lake may have also occurred on numerous occasions during winter from the input of oxygen-saturated rainwater. During the period of ice cover, a total of 159 mm of rainfall was recorded at Peterborough Airport Climatological Station, 30 km southwest of Sharpe Bay. If the rainwater falling on the surface of Sharpe Bay penetrated the ice layer, it would represent an oxygen input of approximately 0.14 mg $\cdot L^{-1}$. This was about eight times the calculated oxygen loss to white ice formation from slushing, and this contribution would increase considerably if runoff from the watershed was included. Winter rainfall events in this climatological region are not uncommon (Adams 1978).

Discussion

In summer, close agreement existed between the hypolimnetic oxygen depletion rate calculated from oxygen profiles and that calculated from WOD and SOD (Table 4). However, this was not the case for the lake during winter under ice cover when WOD plus SOD greatly overestimated the depletion rate calculated from profiles, this value being much lower than the corresponding summer value. Since volume-weighted WOD and SOD were found to be the same in summer and winter, the large difference between the summer and winter deficits determined from profiles appears to have resulted from a significant influx of oxygen to the lake during that period. The descent of

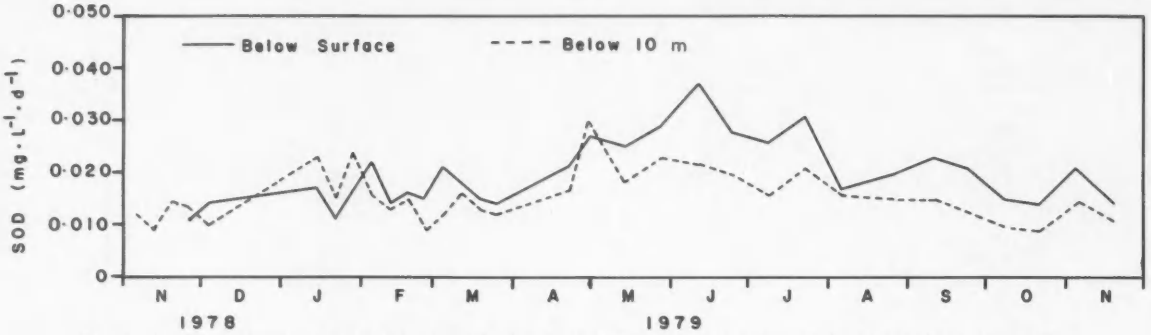

FIG. 4. Temporal patterns of sediment area weighted, volumetric SOD for water volumes below 0 and 10 m in Sharpe Bay.

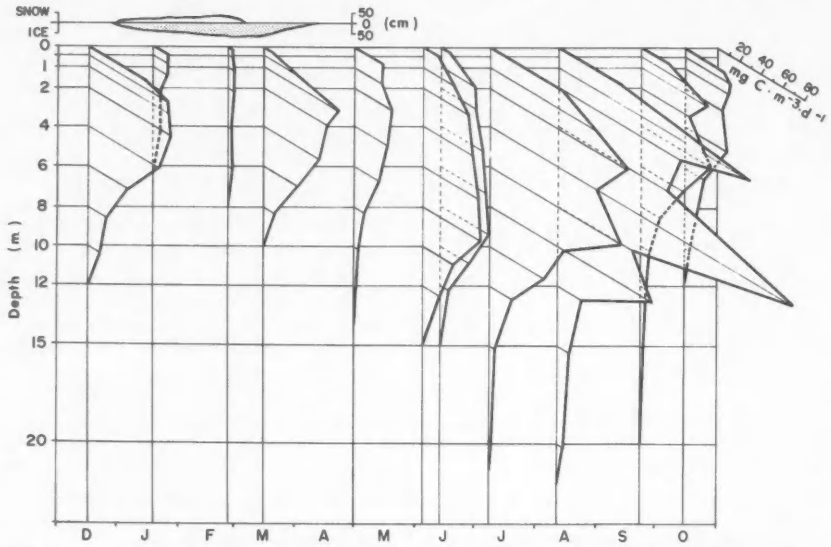

FIG. 5. Temporal patterns of the depth distribution of phytoplankton primary production in Sharpe Bay.

TABLE 4. Summer and winter oxygen depletion rates for Sharpe Bay determined from oxygen profiles and calculated from SOD and WOD.

	Winter (whole lake) ($mg\,O_2 \cdot L^{-1} \cdot d^{-1}$)	Summer (hypolimnion) ($mg\,O_2 \cdot L^{-1} \cdot d^{-1}$)
WOD	0.032	0.027
SOD	0.018	0.020
Total	0.050	0.047
Profile-determined depletion rate	0.003	0.040

the $12\,mg \cdot L^{-1}$ isopleth line (Fig. 2) suggests that oxygenated water mixed to a depth of approximately 15 m during early February. The oxygen depletion rate was calculated from profiles for the water volume below 20 m during winter and found to be $0.031\,mg\,O_2 \cdot L^{-1} \cdot d^{-1}$. This value is closer to the summer hypolimnetic deficit and closely approximates the sum of SOD plus WOD. Lasenby (1975) and Welch et al. (1976) illustrated that other southern Ontario lakes with mean depths similar to that of Sharpe Bay exhibited oxygen depletion rates that were almost identical in summer and winter. If this applies to Sharpe Bay, it appears that the ice cover did not provide an effective barrier against the influx of atmospheric oxygen or oxygen saturated rainwater or meltwater. The possibility that water entered Sharpe Bay through the connecting channel does not seem likely, since the sampling station located near the channel did not exhibit higher oxygen concentrations than the other stations on any given day.

The mean summer hypolimnetic WOD for Sharpe Bay was almost the same as the mean winter WOD (Table 4). This was surprising, since sediment trap studies have shown increased inputs of particulate organic material to the hypolimnia of lakes during summer (Hargrave 1973) which should be accompanied by increased rates of decomposition and oxygen consumption. However, the vertical distribution of WOD in Sharpe Bay during summer showed high rates occurring in the epilimnion, a metalimnetic peak, and comparatively low rates in the hypolimnion. The same distribution has been observed in other water bodies (Lawacz 1969; Riley 1970; Serruya and Serruya 1972; Wetzel et al. 1972; Golterman 1976; Bloesch et al. 1977). Saunders (1976) estimated that up to 90% of the decomposition of organic material, primarily phytoplankton cells, occurs in the mixed layer of the water column and involves the bacterial

degradation of comparatively low molecular weight compounds such as amino acids, carboxylic acids, and sugars. Particulate organic material that has not been decomposed in the epilimnion would settle into the metalimnion but its downward progress may be impeded by cooler, denser water at the top of the hypolimnion. Also, the particles may be smaller in size due to the decomposition that took place in the warmer epilimnion. A longer residence time of the particulate organic material in this area would allow more time for the bacterial colonization and consequently higher decomposition rates in the metalimnion, as we observed. Collins (1963, 1970) noted maximum numbers of heterotrophic bacteria occurring in the metalimnia of thermally stratified lakes. If the particulate material reaching the hypolimnion was in fact readily decomposable, the lower temperatures at these depths may have induced lower decomposition rates and much of the particulate material may have become buried in the sediments.

Hargrave (1973) and Golterman (1976) have suggested that the small proportion of organic matter that reaches the hypolimnion is refractory, consisting of higher molecular weight compounds such as cellulose, chitin, and lignin. They indicated that further decomposition of this material, if it were to occur at all, would require a much longer time period. This implies that biological degradation of organic material is not the cause of the high WOD rates we noted adjacent to the deep sediments. Since the deep sediments in Sharpe Bay were subjected to low oxygen concentrations periodically throughout the year, it is conceivable that reduced material was being mobilized and diffused upward from the sediments (Mortimer 1941, 1942, 1971), producing a high oxygen demand near the sediment surface.

The volume-weighted SOD for Sharpe Bay in winter was very similar to the hypolimnion SOD (Table 4). Although the high summer rates measured for the sediments at 5 m may reflect an increase in the input of sedimenting organic material, they are probably controlled by the temperature of the overlying water. Despite the fact that the range of SOD we observed in Sharpe Bay was comparatively small (0.024–0.051 mg $O_2 \cdot cm^{-2} \cdot d^{-1}$), significant differences were found between sediments at different depths. This suggests that a representative value for the whole lake would have to be determined by "weighting" the SOD measured at each depth by the sediment surface area in that stratum.

Previous studies (Lasenby 1975; Hargrave 1972; Welch and Kalff 1974) have attributed from 20 to 100% of the oxygen depletion in lakes to SOD. These results are difficult to evaluate, since only SOD was measured and compared with the loss rates determined from oxygen profiles. In our study, SOD was six times the winter loss rate determined from profiles but represented approximately 50% of the hypolimnetic rate. Based upon the similarities between winter and summer SOD as well as WOD, it appears that the winter oxygen loss rate determined from oxygen profiles cannot be used as an accurate indicator of lake metabolism, at least for Sharpe Bay. It is not unreasonable to assume that this could apply to other lakes in similar climatic regions. The degree to which oxygen input can influence the depletion rate observed from oxygen profiles is a function of the lake's bathymetry. In Sharpe Bay, the 0–5 m stratum represents approximately 30% of the total volume; therefore, a comparatively small oxygen influx will produce a significant bias.

The excellent agreement between the hypolimnetic loss rate determined from oxygen profiles and the rate obtained by summing SOD and WOD indicates that hypolimnetic deficits may provide a more reliable reflection of lake respiration.

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Effects of Biotic and Abiotic Factors on Growth and Relative Survival of Young American Shad, *Alosa sapidissima*, in the Connecticut River

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Crecco, V. A., and T. F. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. Can. J. Fish. Aquat. Sci. 42: 1640–1648.

We examined the hypothesis that temporal oscillations in zooplankton abundance, river flows, and temperatures in the Connecticut River affect the survival and growth rates of larval and juvenile American shad, *Alosa sapidissima*, among 5-d cohorts. The relative survival rates between newly hatched shad larvae and juveniles were low among early cohorts (May 21 – June 15), but rose rapidly among later cohorts (June 21 – July 6) when river flows were low and temperatures and zooplankton densities were high. Age of larval and juvenile shad was estimated by counting daily rings on sagittal otoliths and age-specific length increments determined by backcalculation techniques. Cohort-specific growth rates of larval shad increased linearly with rising zooplankton densities, and asymptotically with rising river temperatures and declining flows. By contrast, juvenile growth rates among 5-d cohorts showed no significant linear or nonlinear relationships to water temperatures and flows.

Les auteurs étudient l'hypothèse que des oscillations temporelles de l'abondance du zooplancton, des débits fluviaux et de la température dans la rivière Connecticut influent sur les taux de survie et de croissance des larves et des juvéniles de l'alose savoureuse (*Alosa sapidissima*) appartenant à des cohortes âgées de 5 d. Les taux relatifs de survie des larves nouvellement écloses et des juvéniles étaient faibles chez les premières cohortes (21 mai – 15 juin) mais ont rapidement augmenté chez les dernières (21 juin – 6 juillet) quand le débit fluvial était faible et que la température et la densité du zooplancton étaient élevées. L'âge des larves et des juvéniles a été déterminé par dénombrement des anneaux déposés quotidiennement sur les otolithes sagittales et par rétrocalcul des incrémentations de la longueur selon l'âge. Les taux de croissance particuliers à une cohorte de larves ont augmenté de façon linéaire en fonction d'une densité croissante du zooplancton et de façon asymptotique en fonction d'une température croissante des eaux fluviales et d'une baisse du débit. Par contre, le taux de croissance des juvéniles chez les cohortes de 5 d n'a pas montré une importante relation linéaire ou non linéaire en fonction de la température ou du débit des eaux fluviales.

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Year class strength of Connecticut River American shad, *Alosa sapidissima*, appears to be established by the end of the larval period by a complex interrelationship between biotic and abiotic factors mediated by annual changes in egg production (Leggett 1977; Crecco et al. 1982, 1983). June river flow, water temperature, and zooplankton availability have been statistically linked to changes in shad larval mortality and year class variability from 1966 through 1978 (Crecco and Savoy 1984). However, the ecological pathways through which biotic and abiotic factors ultimately affect recruitment are so complex that a number of recruitment hypotheses (Hjort 1926; Cushing and Dickson 1976; Frank and Leggett 1983) appear to be consistent with our present knowledge. The main problem is that the testing and ultimate rejection of many shad recruitment hypotheses has progressed very slowly mainly because only a single pair of larval and/or juvenile abundance and mortality estimates are produced each year. A method of generating multiple data points on mortality and growth would permit a more rapid evaluation of these hypotheses, leading eventually to a more unified approach to separating natural variations in shad recruitment from those attributed to fishing, dams, and other man-made impacts.

The discovery of daily growth rings on the otoliths of many fish species (Pannella 1971; Brothers et al. 1976; Taubert and Coble 1977) not only provided a method of generating multiple data points, but also furnished a valuable tool with which to analyze within-season changes in growth and survival of larval and juvenile American shad. The otolith technique allows larvae and juveniles to be separated into specific cohorts depending on age at capture, so that variability in daily growth rates among the cohorts can be analyzed and perhaps related to changes in environmental conditions. More importantly, the otolith method can be used to estimate the relative survival and contributions of these larval cohorts to juvenile relative abundance some 2–3 mo later. This serves as a vital link to enhance our understanding of the recruitment mechanisms, as juvenile shad relative abundance in the Connecticut River was shown to be highly correlated with adult recruitment 4–6 yr later (Crecco et al. 1983).

Our study was primarily designed to examine how short-term

changes in environmental factors affect within-year changes in growth and relative survival of larvae from the 1983 year class of shad in the Connecticut River. We used the otolith aging technique to backcalculate daily growth (millimetres per day) of American shad larvae from consecutive 5-d cohorts. We then assessed the extent to which fluctuations in river temperatures, flows, and zooplankton densities during May and June affect larval growth rates among the various cohorts. Finally, the age and growth rates of juvenile American shad were estimated by the otolith method, and relative survival rates from larval to the juvenile stage were estimated and related to short-term changes in hydrographic conditions in the river.

Methods

Data Collection

American shad larvae were sampled during daylight in the Connecticut River with a 6.1-m plankton bag seine (2.4 m deep, wing and bag mesh of 0.505 mm) and 30-m lead ropes from May 15 to July 22, 1983. One seine haul was taken weekly at each of eight sites located north of the Enfield Dam (river km 88). The method by which shad larvae were collected is described in Crecco et al. (1983). Approximately 10–20 American shad larvae were removed from each sample and frozen for otolith age determination. All remaining larvae were transferred to jars containing 4% formalin.

Juvenile American shad were collected weekly at seven stations located below the Holyoke Dam from July 15 through October 15, 1983. Juvenile sampling at each station occurred during daylight hours with a 15.2-m nylon bag seine (4.8-mm mesh, 2.4-m deep, 2.4-m bag) and 30-m lead ropes similar to that used in a previous juvenile survey (Marcy 1976). All alosid juveniles were placed in jars containing 4% formalin. The crystalline nature of juvenile otoliths allowed their preservation in formalin without dissolution.

The composition and density (number per cubic metre) of river zooplankton were monitored weeky from May 15 through July 15, 1983, at four of the larval seine stations. Zooplankton were sampled with a 13.0-cm Clark–Bumpus plankton sampler fitted with a 0.08-mm-mesh net. Duplicate 1-min tows were made in a downstream direction about 1 m below the surface. Mean density of each sample was estimated by direct proportion between the mean number of organisms counted in two to three aliquots and the volume of the river water sampled. The coefficient of variation (standard deviation/mean) of the geometric mean zooplankton densities varied from 20 to 30% among weekly collections. Only cladocerans, copepods, and immature insects were identified to genus and enumerated, as American shad larvae feed almost exclusively on these taxa (Maxfield 1953; Crecco and Blake 1983).

Otolith Age Determinations

A total of 387 American shad larvae were chosen randomly from all stations and weekly collection dates for age and growth analysis. Larval age (days) was estimated by counting growth rings on sagittal otoliths which were embedded in histoclad mounting medium and covered with a glass cover slip. By contrast, 179 pairs of juvenile otoliths were air dried and mounted on a glass slide with butyl acetate. After drying for 1 wk, juvenile otoliths were placed in a grinding apparatus (Neilson and Geen 1981) where successive layers were ground to the midplane to enhance the visibility of the rings. The rings on

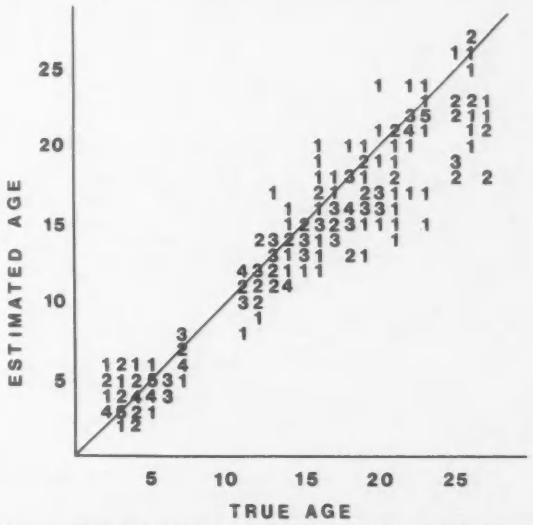

FIG. 1. Relationship between the number of otolith rings and the true age of hatchery-reared American shad larvae. The numbers denote the sample size at each age with a 45° transfer line.

larval and juvenile shad otoliths were highly visible in most specimens, which is characteristic of otoliths of other herring larvae (Brothers et al. 1976).

Growth rings on larval and juvenile otoliths were counted three times under transmitted light (100×), and the final age was regarded as the mean of the three estimates. Otolith half-length and distance from the focus to each growth ring were measured in micrometre units. Backcalculated lengths (millimetres total length, TL) were estimated daily from ages 4–8 d and weekly from ages 7, 14, 21 d, etc., by the Lea method (Ricker 1971). A constant y-intercept value of 8.0 mm (TL) was chosen for shad larvae at hatching (Maxfield 1953; Lippson and Moran 1974). Knowing the age and date of capture, each larva and juvenile was assigned to one of nine 5-d cohorts from May 19 through July 3, 1984.

The extent to which sagittal otoliths provide an accurate description of the age and growth of larval and juvenile American shad depends on the assumptions that each growth ring is deposited daily, and that the otolith grows in direct proportion to the body length of the fish. To test these assumptions, otolith age determinations were made in 1983 on 248 known-age shad larvae from the Benner Springs State Fish Hatchery, Pennsylvania. Both sagittal otoliths were removed from larvae ranging from 9 to 13 mm (TL) and aged in the same manner as American shad larvae from the Connecticut River. Neither the length nor the age of the hatchery fish was known to the observer during the aging process. There was a significant linear relationship ($r = 0.89$, $P < 0.001$) between the number of sagittal rings and the true daily age (Fig. 1), indicating that the chronological ages from the otoliths were good estimates of the true ages. The linear regression between otolith diameter and larval length was significant for fish grouped by age ($r = 0.93$, $P < 0.001$) (Fig. 2) and ungrouped ($r = 0.77$, $P < 0.001$) with the y-axis intercepts for grouped (9.06 mm) and ungrouped (8.7 mm) data being very close to the mean length (8.0 mm) at hatching, indicating that growth increments on the otolith reflect growth changes of larval American shad. In addition, we found that

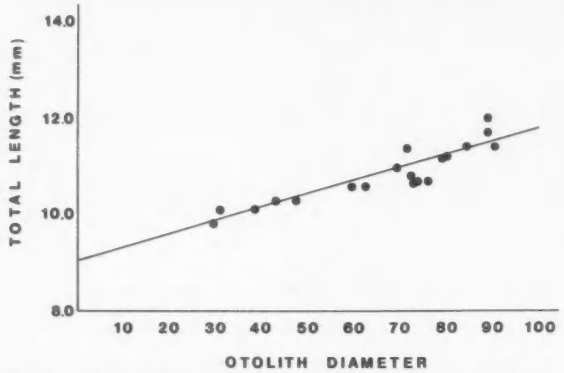

FIG. 2. Linear relationship between otolith diameter (μm) and larval length of hatchery-reared American shad larvae. These data are grouped by age.

over 85 and 93% of the 248 known-age larvae were correctly assigned into 5- and 7-d cohorts, respectively (Savoy and Crecco 1986), thereby justifying the use of 5- and 7-d cohorts in this study.

Data Analysis

Age-specific instantaneous growth rates (millimetres per day) were estimated based on backcalculated length-at-age data from 4 to 8 d and for each 7-d interval thereafter (i.e. 7–14, 14–21, 21–28 d, etc.) by the method of Ricker (1975):

$$(1) \quad G_{it} = \mathrm{LN}(L_{it+1}) - \mathrm{LN}(L_t)/t + 1 - t$$

where G_{it} = instantaneous growth rate of a larva or juvenile from the ith cohort between the ages t and $t + 1$, L_{it+1} = total length (millimetres) of a larva or juvenile from the ith cohort at age $t + 1$, L_{it} = total length (millimetres) of a larva or juvenile from the ith cohort at age t, and $t + 1 - t$ = length of time (days) between L_t and L_{t+1}. Mean age-specific growth rates (G_{it}) and standard deviations (SG_{it}) were calculated based on all shad larvae and juveniles within each 5-d cohort.

Knowledge of age-specific growth rates for larval and juvenile American shad is important for analyzing the patterns in early life history growth and for constructing accurate survivorship curves (Farris 1960; May 1974). We fitted the backcalculated length–age data from each 5-d cohort to the Gompertz growth equation:

$$(2) \quad L_t = L_0 e^{K(1-e^{-at})}$$

as was recommended for larval and juvenile growth analysis (Kramer and Zweifel 1970; Zweifel and Lasker 1976). The Gompertz equation was fitted to the data with a nonlinear least square regression (Ralston and Jenrich 1978) in which the initial parameter estimates (L_0', a', K') were estimated by the regression techniques of Ratkowsky (1983).

One-way analysis of variance and Scheffe's test of multiple comparisons (Snedecor and Cochran 1980) were conducted to examine whether larval growth rates differed significantly ($p < 0.05$) among 5-d cohorts. All statistical tests were performed separately on growth data from the four age intervals (4–8, 7–14, 14–21, and 21–28 d) to evaluate the extent to which growth differences among 5-d cohorts were related to larval age.

Mean instantaneous growth rates (G_{it}) of American shad larvae for each 5-d cohort were also examined against short-term changes in river flows and temperatures with linear and nonlinear regression analysis. The instantaneous growth rates were also estimated separately on the same age intervals used in the analysis of variance. This procedure was done to determine whether growth rates of younger and older shad larvae respond differently to changes in abiotic factors. River flow (cubic metres per second) and water temperature (degrees Celsius) were chosen as environmental variables because they were recorded daily close to major shad spawning areas. River flows were recorded daily at Thompsonville, Connecticut (river km 89), by the U.S. Geological Survey (1983), whereas water temperatures were taken daily at the Holyoke Dam (river km 120) by the Holyoke Water Power Company (Northeast Utilities Corporation, unpubl. reports).

There are a number of ways in which fluctuations in river flows and temperatures can be related to age- and cohort-specific changes in larval growth rates. In this paper, we considered the median day (day 3) within each 5-d cohort as a reasonable starting date with which to estimate flow and temperature conditions during larval growth. By setting the starting date for each cohort at day 3, mean daily river flow and temperature were calulated for the dates inclusive within each of the four age intervals. These mean flow and temperature values were considered as independent variables in the linear and nonlinear regression analysis. The coefficient of variations about the 5-d mean temperatures and flows seldom exceeded 15%.

We also evaluated whether age-specific changes in larval growth rates among cohorts were related to fluctuations in river zooplankton densities. However, because river zooplankton was monitored weekly, it was necessary to recompute instantaneous growth rates for 7-d rather than 5-d cohorts. Like the previous analysis, both linear and nonlinear regression analyses were used to examine the extent to which age-specific larval growth rates were related to river zooplankton availability.

Once the 387 shad larvae and 179 juveniles had been aged and placed within 5-d cohorts, the relative survival rate (S_i) for larval shad for each 5-d cohort was estimated by

$$(3) \quad S_i = J_i/L_i$$

where J_i = the total number of juvenile shad placed within the ith 5-d cohort and L_i = the total number of larval shad placed within the ith 5-d cohort. Changes in relative survival rates among all cohorts were regressed against temporal fluctuations in river flows and temperatures at 3- and 7-d intervals before and after larval emergence. Support for the hypothesis that abiotic factors during the early larval stages have the greatest influence on survival to the juvenile stage and beyond would be demonstrated if the highest correlations between relative survival and the two abiotic factors occurred some 3–14 d after larval emergence. Conversely, if the highest correlations occurred during the intervals consistent with the egg stage (−21 to −3 d) or juvenile stage (28–42 d), the analysis would not support the hypothesis.

Results

Length Increments for Larval and Juvenile Shad

Backcalculated length–age data for 387 shad larvae and 179 shad juveniles were partitioned among 5-d cohorts (Tables 1 and 2). Age-specific length increments for shad larvae increased slowly for cohorts emerging before June 6, and then more abruptly for all cohorts thereafter. By contrast, length incre-

TABLE 1. Mean ($\bar{x}$) backcalculated total lengths (mm) for American shad larvae among 5-d cohorts (SE = standard error; N = number of observations).

5-d cohort	Age (d)							
	4	5	6	7	8	14	21	28
May 22								
$\bar{x}$	10.8	11.1	11.4	11.7	12.1	14.2	16.7	18.4
SE	0.50	0.53	0.58	0.64	0.67	1.02	1.44	1.27
N	6	6	6	6	6	6	6	3
May 27								
$\bar{x}$	10.6	10.9	11.2	11.5	11.8	14.0	16.8	18.7
SE	0.10	0.11	0.11	0.11	0.12	0.21	0.36	0.88
N	16	16	16	16	16	16	14	3
June 1								
$\bar{x}$	10.6	10.9	11.2	11.5	11.8	14.0	17.7	23.1
SE	0.07	0.07	0.07	0.08	0.09	0.17	0.39	0.40
N	39	39	39	39	39	28	18	4
June 6								
$\bar{x}$	10.7	11.0	11.4	11.8	12.2	15.2	19.6	24.8
SE	0.04	0.05	0.06	0.07	0.09	0.18	0.18	0.55
N	81	81	81	81	78	67	44	6
June 11								
$\bar{x}$	10.5	10.8	11.2	11.7	12.1	15.6	18.4	23.1
SE	0.04	0.05	0.07	0.08	0.10	0.18	0.34	1.39
N	67	67	66	62	62	48	16	4
June 16								
$\bar{x}$	10.3	10.7	11.1	11.6	12.0	15.4	18.8	21.1
SE	0.04	0.04	0.05	0.06	0.07	0.14	0.32	0.82
N	92	90	87	85	81	67	25	4
June 21								
$\bar{x}$	10.0	10.3	10.7	11.1	11.4	14.3	18.1	
SE	0.08	0.10	0.11	0.12	0.14	0.26	0.77	
N	35	35	35	35	35	32	12	
June 26								
$\bar{x}$	10.2	10.5	10.9	11.3	11.7	15.1	19.5	
SE	0.06	0.07	0.08	0.09	0.11	0.19	0.60	
N	36	36	36	36	36	30	9	
July 1								
$\bar{x}$	10.1	10.5	10.8	11.2	11.6	15.1	19.0	
SE	0.09	0.11	0.12	0.14	0.15	0.30	1.00	
N	14	14	14	14	13	7	2	

ments of juvenile shad showed no consistent differences among 5-d cohorts.

Mean length increments of shad larvae among all cohorts were relatively low from 4 to 8 d (0.38 mm/d), rising rapidly from 8 to 21 d (0.52 mm/d), and then declining slightly (0.49 mm/d) just before (21–28 d) metamorphosis (Fig. 3). After metamorphosis, juvenile shad apparently undergo a second sigmoid growth phase, as indicated by a rapid increase in length (1.05 mm/d) from 28 to 70 d, after which length increments declined steadily to a theoretical asymptote (90–110 mm) at about 77–100 d. The age-specific patterns of larval and juvenile growth among 5-d cohorts were well described by the Gompertz equation as indicated by high r^2 for all cohorts (Table 3 and 4).

Instantaneous Growth Rates

Mean instantaneous growth rates (G_{it}) were computed among 5-d cohorts for the larval age intervals 4–8, 7–14, 14–21, 21–28 d and for successive 7-d intervals during juvenile development (Tables 5 and 6). One-way analysis of variance on each age interval indicated that larval G_{it} age interval values differed significantly among 5-d cohorts for larval 7–14 and 14–21 d. The Scheffe multiple comparison test detected significant growth differences among early larvae (4–8 d) at the $p < 0.10$ level, indicating that growth rates of young shad larvae hatched early (May 22, May 27, June 1) were lower than for newly hatched larvae during late June and July following abrupt increases in river temperature. Mean growth rates of first-feeding larvae (7–14 d) exhibited more apparent differences among 5-d cohorts than did larvae 4–8 d. The Scheffe test showed that G_{it} values for larvae 7–14 d were significantly lower for early cohorts (May 22, May 27) than for cohorts hatched after mid-June following the rapid rise in water temperature. The trend between larval growth and rising water temperatures was corroborated further by significant growth difference between some of the early and late cohorts for older (14–21 d and 21–28 d) larvae.

TABLE 2. Mean backcalculated lengths (mm) for American shad juveniles among 5-d cohorts (N = number of observations).

5-d cohort	Age (d)								
	35	42	49	56	63	70	77	84	91
June 6									
$\bar{x}$	34.3	43.6	52.4	61.9	73.6	81.6	89.2	96.1	88.0
SE	1.14	1.70	1.88	2.12	4.49	5.46	6.19	7.19	0.00
N	7	7	7	7	3	3	3	3	1
June 11									
$\bar{x}$	32.2	40.9	50.3	58.9	65.0	72.0	82.1	77.5	77.3
SE	0.81	1.18	1.80	3.37	4.14	4.37	10.29	5.46	0.00
N	13	13	13	9	6	6	3	2	1
June 16									
$\bar{x}$	32.0	40.3	48.6	56.1	62.7	67.9	69.7	72.4	70.6
SE	0.35	0.38	0.60	0.84	1.12	1.57	1.76	2.12	0.92
N	29	29	29	23	22	19	14	10	6
June 21									
$\bar{x}$	31.5	39.5	47.8	54.9	61.2	64.4	69.1	71.4	72.7
SE	0.33	0.51	0.61	0.55	0.72	0.85	0.99	1.31	2.11
N	49	49	49	46	44	28	28	16	7
June 26									
$\bar{x}$	31.7	40.2	48.5	56.1	62.7	68.5	71.8	77.9	83.5
SE	0.25	0.35	0.54	0.66	0.82	0.95	1.14	1.96	2.27
N	53	53	53	53	51	51	37	22	6
July 1									
$\bar{x}$	31.7	40.4	48.2	55.5	62.3	68.6	74.2	78.7	83.5
SE	0.37	0.58	0.75	0.98	1.28	1.42	1.56	2.55	3.50
N	22	22	22	21	20	20	17	10	2
July 6									
$\bar{x}$	33.6	43.3	51.7	59.7	67.0	73.4	79.7	83.8	87.4
SE	0.72	1.20	1.37	1.05	1.20	0.99	0.93	1.17	0.00
N	6	6	6	6	6	6	5	2	1

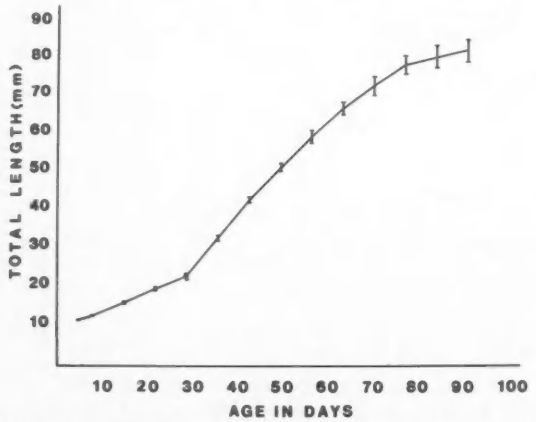

FIG 3. Mean total lengths of larval and juvenile American shad with age (d) (bars = ±1SD).

Instantaneous growth rates for juvenile shad were high among all cohorts from 28 to 56 d, declining steadily as juvenile shad approach the age (77–100 d) at which emigration occurred (Table 6). Unlike the larval growth rates, age-specific growth of juveniles showed no consistent differences between early and late cohorts.

TABLE 3. Estimates of parameters for the Gompertz equation for larval growth by 5-d cohorts (L_0 = mean length of newly hatched shad larva (8.0 mm), where K and a were estimated by nonlinear regression analysis, t = age of fish, $L_t = L_0 e^{K(1-e^{-at})}$, and r^2 = coefficient of determination).

5-d cohort	Sample size	L_0	K	a	r^2
May 27	16	8.0	1.025	0.065	0.90
June 01	39	8.0	1.602	0.035	0.88
June 06	81	8.0	1.756	0.035	0.91
June 11	67	8.0	1.429	0.045	0.91
June 16	92	8.0	1.367	0.042	0.92
June 21	35	8.0	1.579	0.034	0.85
June 26	36	8.0	2.206	0.025	0.93
July 01	14	8.0	1.724	0.033	0.93

Larval and Juvenile Growth vs. River Flow, Temperature, and Zooplankton

Age-specific changes in larval growth among 5-d cohorts were related to short-term fluctuations in river flow and temperature with linear and nonlinear regression analyses. We found that cohort-specific growth changes among young (4–8 d) and intermediate (7–14 and 14–21 d) aged larvae followed a sig-

TABLE 4. Estimates of parameters for the Gompertz equation for juvenile growth by 5-d cohorts (L_0 = mean length at metamorphosis (24.0 mm), where K and a were estimated by nonlinear regression analysis, t = age of fish, t_0 = age of fish at metamorphosis (28 d), $L_t = L_0 e^{K(1-e^{-at})}$, and r^2 = coefficient of determination).

5-d cohort	Sample size	L_0	L	K	a	r^2
June 06	7	24.0	102	1.449	0.038	0.63
June 11	13	24.0	87	1.283	0.042	0.62
June 16	29	24.0	82	1.233	0.043	0.90
June 21	49	24.0	84	1.256	0.039	0.90
June 26	53	24.0	99	1.414	0.033	0.88
July 01	22	24.0	103	1.460	0.031	0.91
July 06	6	24.0	104	1.464	0.035	0.99

moid trend with water temperatures and flow for which the nonlinear logistic equation,

$$(4) \quad G_{it} = a_0/1 + \exp(B - Yx)$$

where a_0 = maximum growth rate with respect to water temperatures and flows, B = growth rate at the inflection point, Y = rate of exponential decay, and x = either temperature or flow, provided the best overall fit (Table 7). For each cohort, growth rates of all except the oldest larvae (21–28 d) showed a significant sigmoid increase with rising water temperatures. Growth rates among 4–21 d larvae rose steadily as temperatures in the river increased from 15 to 20°C, and then more slowly as water temperatures exceeded 23°C. Cohort growth rates among older larvae (21–28 d) increased with water temperature, but the relationship was not significant.

The relationship between larval growth and river flows was of the same magnitude but different in direction from the growth–temperature relationship. The growth–flow relationships for shad larvae between 4 and 21 d were well described by the logistic model (Table 7). Low instantaneous growth rates among early cohorts (May 22, May 27, June 1) were associated with high (566.3–1132.7 m^3/s) and fluctuating river flow conditions, whereas the relatively higher growth rates among later larval cohorts (June 21, June 26, July 1) were coincident with river flows of less than 283.2 m^3/s. These data suggest that low growth rates of newly hatched (4–8 d) and intermediate aged (7–14 and 14–21 d) shad larvae from early cohorts were largely due to high river flows and low water temperatures.

When the same linear and nonlinear analyses were conducted on juvenile growth, there were no consistent relationships between cohort growth rates and temporal changes in either river flows or temperatures (Table 8). Therefore, fluctuations in river flows and temperatures during July and August appear to exert little effect on juvenile growth rates among 5-d cohorts.

The degree to which larval growth rates among 7-d cohorts were related to zooplankton variability depended on the age interval (Table 7). There was always a positive correlation between larval growth and zooplankton abundance, but it was significant only for 4–8 and 7–14 d larvae, the former relationships being nonlinear.

Relationship among Relative Survival, Water Temperature, and Flow

The relative survival rate between newly-hatched larvae and juveniles differed among 5-d cohorts, being zero for the three early cohorts, increasing slowly from June 1 to June 16 (Table 9). After the June 16 cohort, relative survival rates rose abruptly by almost an order of magnitude, with 73% of the juveniles originating from the last four cohorts. The low survival rates among early cohorts were associated with low water temperatures (10–14°C), high river flows (566.3–1132.7 m^3/s), and low densities of river zooplankton (150–300/m^3). By contrast, the success of the later cohorts (June 21 – July 6) took place when temperatures and zooplankton were high, and river flows were low. These data provide further evidence that growth and survival of shad larvae are directly linked to water temperature and flow conditions.

To further examine the extent to which abiotic factors were coupled with larval and juvenile survival rates, we correlated the log + 0.01 of cohort survival against the water temperatures and flows at 3- and 7-d intervals before and after the median date of each 5-d cohort. Relative survival rates among 5-d cohorts were positively correlated with intervals of water temperature

TABLE 5. Mean instantaneous growth rates (G_{it}) of larval shad among 5-d cohorts (N = number of observations).

5-d cohort	Age interval (d) 4–8	7–14	14–21	21–28
May 22				
$\bar{x}$	0.0287	0.0282	0.0220	0.0210
SE	0.0117	0.0115	0.0090	0.0121
N	6	6	6	3
May 27				
$\bar{x}$	0.0269	0.0277	0.0265	0.0213
SE	0.0005	0.0015	0.0012	0.0012
N	16	16	14	3
June 01				
$\bar{x}$	0.0270	0.0288	0.0321	0.0322
SE	0.0007	0.0012	0.0016	0.0033
N	39	28	18	4
June 06				
$\bar{x}$	0.0334	0.0351	0.0338	0.0299
SE	0.0011	0.0011	0.0013	0.0015
N	81	69	46	8
June 11				
$\bar{x}$	0.0351	0.0394	0.0303	0.0331
SE	0.0013	0.0010	0.0025	0.0018
N	67	51	18	6
June 16				
$\bar{x}$	0.0372	0.0401	0.0311	0.0247
SE	0.0008	0.0008	0.0010	0.0020
N	92	74	30	5
June 21				
$\bar{x}$	0.0331	0.0357	0.3279	0.0000
SE	0.0013	0.0014	0.0154	0.0000
N	35	32	12	0
June 26				
$\bar{x}$	0.0355	0.0402	0.0362	0.0000
SE	0.0018	0.0012	0.0016	0.0000
N	36	30	9	0
July 01				
$\bar{x}$	0.0339	0.0412	0.0380	0.0000
SE	0.0016	0.0019	0.0051	0.0000
N	14	8	2	0

TABLE 6. Mean instantaneous growth rates (G_{it}) of juvenile shad among 5-d cohorts (N = number of observations).

5-d cohort	Age interval (d)							
	35–42	42–49	49–56	56–63	63–70	70–77	77–84	84–91
June 6								
$\bar{x}$	0.03415	0.02645	0.02395	0.01935	0.01456	0.01265	0.01057	0.00971
SE	0.00100	0.00156	0.00219	0.00130	0.00135	0.00115	0.00101	0.00000
N	7	7	7	3	3	3	3	1
June 11								
$\bar{x}$	0.03396	0.02928	0.02347	0.01771	0.01511	0.01133	0.01031	0.00994
SE	0.00073	0.00141	0.00092	0.00087	0.00120	0.00123	0.00146	0.00000
N	13	13	9	6	6	3	2	1
June 16								
$\bar{x}$	0.03295	0.02663	0.02139	0.01591	0.01193	0.00861	0.00709	0.00639
SE	0.00074	0.00068	0.00049	0.00068	0.00076	0.00042	0.00042	0.00035
N	28	28	23	22	19	14	10	6
June 21								
$\bar{x}$	0.03205	0.02736	0.02093	0.01619	0.01266	0.01003	0.00908	0.00591
SE	0.00100	0.00094	0.00045	0.00057	0.00050	0.00046	0.00053	0.00036
N	49	49	46	44	28	28	17	7
June 26								
$\bar{x}$	0.03359	0.02676	0.02067	0.01602	0.01275	0.01090	0.00888	0.00749
SE	0.00059	0.00056	0.00044	0.00033	0.00042	0.00030	0.00034	0.00067
N	53	53	53	51	51	37	22	6
July 1								
$\bar{x}$	0.03446	0.02535	0.02011	0.01621	0.01367	0.01166	0.01006	0.00776
SE	0.00097	0.00078	0.00058	0.00050	0.00050	0.00038	0.00065	0.00092
N	22	22	21	20	20	17	10	2
July 6								
$\bar{x}$	0.03604	0.02541	0.02047	0.01666	0.01293	0.01185	0.00622	0.00794
SE	0.00158	0.00072	0.00211	0.00099	0.00067	0.00056	0.00219	0.00000
N	5	5	5	5	5	5	2	1
July 11								
$\bar{x}$	0.02973	0.02174	0.01887	0.01210	0.01115	0.00833	0.00787	0.00927
SE	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
N	1	1	1	1	1	1	1	1

TABLE 7. Estimates of parameters for logistic and exponential equations relating larval growth from various cohorts to water temperature, flow, and zooplankton density (a_0, B, and Y estimated by nonlinear regression analysis; r^2 = coefficient of determination; $*P < 0.05$).

Age interval (d)	a_0	B	Y	r^2
Logistic equation: larval growth vs. water temperature				
4–8	0.045	0.810	−0.084	0.82*
7–14	0.062	1.360	−0.071	0.84*
14–21	0.067	2.474	−0.096	0.72*
21–28	0.034	8.652	−0.426	0.31
Logistic equation: larval growth vs. river flow				
4–8	0.040	−2.286	0.00004	0.87*
7–14	0.057	−1.043	0.00003	0.86*
14–21	0.039	−3.744	0.00001	0.66*
21–28	0.046	−1.145	0.00007	0.50*
Exponential equation: larval growth vs. zooplankton abundance				
4–8	0.026	0.0005	—	0.47*
7–14	0.026	0.0007	—	0.49*
14–21	0.026	0.0003	—	0.09
21–28	0.021	0.0005	—	0.31

and inversely correlated with intervals of river flow (Fig. 4). The highest inverse correlations with river flows occurred 7–14 d after larval emergence. Likewise, the highest correlations between survival and water temperatures took place during larval development (3–7 d), although high and persistent correlations were evident some 14 d before and 21 d after hatching. Correlation coefficients coincident with juvenile development (28–42 d) were always low, suggesting that temperature and flow conditions during juvenile development have little effect on larval to juvenile survival.

Discussion

Our results show that the otolith aging technique can be used effectively to analyze the effects of short-term hydrographic fluctuation on larval shad growth and mortality. It is less certain, however, to what degree the otolith aging method can be generalized to growth studies of other fishes, since there is some controversy over whether otolith rings are always daily and reflect the short-term somatic growth patterns of young fish (Brothers et al. 1976; Marshall and Parker 1982). Nevertheless, there are few effective alternatives to the otolith method for analyzing early life history growth patterns. Given that larval

TABLE 8. Linear correlation analysis between age-specific growth of juvenile shad among 5-d cohorts and short-term changes in river temperature and flow (*$P < 0.05$).

	Correlation coefficient	
Age interval (d)	River temperature	River flow
35–42	−0.10	+0.81*
42–49	+0.30	−0.52
49–56	+0.50	−0.14
56–63	+0.88*	+0.36
63–70	+0.32	+0.78*
70–77	−0.51	−0.10
77–84	−0.37	−0.42
84–91	+0.41	+0.60

TABLE 9. Relative survival rate of juvenile American shad among 5-d cohorts. The 387 larvae and 179 juveniles were backcalculated to a 5-d cohort based on otolith determinations. Relative survival is the number of juveniles divided by the number of larvae within each cohort.

5-d cohort	Number of newly hatched larvae	Number of juveniles	Relative survival
May 22	6	0	0.0
May 27	16	0	0.0
June 01	39	0	0.0
June 06	81	7	0.086
June 11	67	13	0.194
June 16	92	29	0.315
June 21	35	49	1.400
June 26	36	53	1.470
July 01	14	22	1.570
July 06	1	6	6.000
Total	387	179	

shad growth rates are age specific, nonlinear, and highly variable among 5-d cohorts, it is unlikely that length–frequency analysis alone would provide accurate information on age and growth with which to estimate age-specific surviorship (Farris 1960; Dahlberg 1979).

Climatic events influence year class strength of many fish stocks (Hjort 1926; Lasker 1975; Cushing and Dickson 1976). However, only recently have integrated field studies been initiated to elucidate causal pathways through which climatic variability affects larval mortality and ultimately recruitment (Lasker 1975; Fortier and Leggett 1983; Leggett et al. 1984). The central theme of most climate–fisheries studies is that food availability and predation are the proximal factors determining the extent of larval survival and growth, whereas short-term climatic events are the forcing mechanisms that drive the system (Legendre and Demers 1984). Correlation studies of Connecticut River shad have linked fluctuations in June river flows and temperatures to year class variability (Marcy 1976) and to deviations in the stock–recruitment relationship (Leggett 1977). Integrated field studies (Crecco et al. 1983; Crecco and Savoy 1984) have demonstrated further that shad year class strength is established before the juvenile stage, and that the failure of the 1982 year class was associated with high June river flows, low temperatures, and high larval mortality, whereas conditions

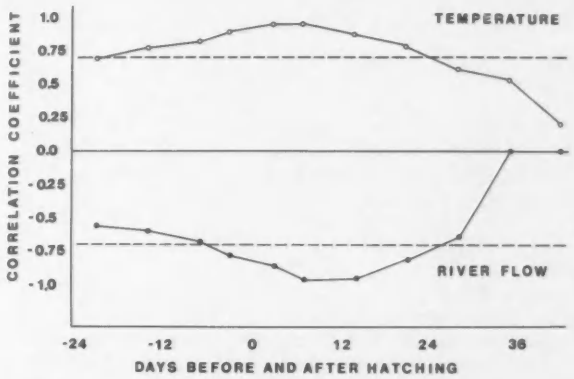

FIG. 4. Correlation coefficients (r^2) for the relationship between short-term changes in river temperature (°C) and flow (m^3/s) and relative survival among 5-d cohorts. Broken lines indicate significant ($P < 0.05$) correlations.

were completely reversed for the strong 1980 year class. Results from this study indicate that not only is shad year class fixed by the juvenile stage, but that juvenile relative abundance in 1983 was dominated by 5-d cohorts which emerged near the end of June (Table 9), when river flows were low and temperatures were high. These data provide a reasonable explanation for the weakness of the parent–progeny relationship for American shad, as well as the necessary information with which to develop a predictive climate–fisheries model.

An understanding of the mechanisms by which hydrographic fluctuations in the river influence larval shad growth and mortality rates is confounded by the high degree of colinearity among river flow, temperature, transparency, and zooplankton density. For example, June water temperature, transparency, and zooplankton abundance usually increase sharply after June flows decline below 339.8 m^3/s (Crecco and Savoy 1984). Therefore, it is unclear whether the significant inverse relationship between river flow and larval growth is caused directly by flow, or by an increase in larval metabolism resulting from rising temperatures, or to improved feeding conditions brought about by high visibility and densities of preferred zooplankton.

We found that cohort-specific growth rates among first-feeding shad larvae (4–14 d) were strongly related to oscillations in river flow, temperature, and zooplankton densities (Table 7), whereas the same relationships among older larvae (21–28 d) and juveniles (Table 8) were weak. One explanation for these poor relationships is that older larvae and juveniles are present from July through October when river flows and water temperatures show minor fluctuations relative to the months of May and June. There is convincing evidence, however, that juvenile shad growth rates are mainly governed by intraspecific competition rather than by abiotic factors. This growth compensation hypothesis is supported by significant inverse correlations between juvenile mean lengths during emigration and adult shad abundance in the Holyoke Pool (Watson 1970; Rosen 1982) and between juvenile relative growth and relative abundance in the lower Connecticut River (Marcy 1976; Leggett 1977; Crecco et al. 1981, 1982).

The age-specific length increments of shad larvae and juveniles followed a sigmoid trend which was well described by the Gompertz equation (Tables 3 and 4). One growth stanza was evident from hatching to metamorphosis and another through-

out juvenile development (Fig. 3). This confirms the pattern reported previously (Crecco et al. 1983). Hunter (1976), Zweifel and Lasker (1976), and Lough et al. (1982) have also demonstrated that larval growth of marine herring follows a sigmoid pattern. Shad larvae reared in earthen ponds (Maxfield 1953), rearing troughs (Wiggins et al. 1984), and juvenile shad sampled from the Connecticut River (Marcy 1976; Rosen 1982; Crecco et al. 1983) also exhibited sigmoid growth.

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Density-Dependent Catchability and Its Potential Causes and Consequences on Connecticut River American Shad, *Alosa sapidissima*

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Crecco, V. A., and T. F. Savoy. 1985. Density-dependent catchability and its potential causes and consequences on Connecticut River American shad, *Alosa sapidissima*. Can. J. Fish. Aquat. Sci. 42: 1649–1657.

Using commercial catch per unit effort data (C/f) and relative shad population size, we assessed the hypothesis that commercial catchability coefficients for Connecticut River American shad, *Alosa sapidissima*, are inversely related to female shad population size. Daily female catch per gillnet drift and commercial effort data from 1978 through 1980 were also used to evaluate the nonrandom search behavior of fishermen, as well as the extent of temporal heterogeneity of the female shad population. Commercial catchability coefficients were inversely related to female shad population size, the relationship being well described by a power function with an exponent (B) of −0.743. Commercial C/f data were asymptotically and not linearly related to changes in the female population size, indicating that commercial C/f data underestimate percent changes in the female shad population. The inverse relationship between catchability and female population size was not due to serial improvements in gear technology, but rather to the ability of commercial fishermen to differentially exploit patches of female American shad during their upriver migration.

À l'aide des données sur les prises commerciales par unité d'effort (C/f) et la taille relative de la population d'aloses, les auteurs ont évalué l'hypothèse selon laquelle les coefficients de capturabilité commerciale de l'alose savoureuse (*Alosa sapidissima*) peuplant la rivière Connecticut sont en corrélation inverse avec le nombre de femelles. Les prises quotidiennes de femelles par filet maillant dérivant et les données commerciales sur l'effort déployé de 1978 à 1980 ont aussi servi à l'évaluation du comportement de recherche non aléatoire des pêcheurs et de l'importance de l'hétérogénéité temporelle de la population d'aloses femelles. Les coefficients de capturabilité commerciale étaient en corrélation inverse avec le nombre de femelles : une fonction de puissance, où l'exposant $B = -0{,}743$, décrivant bien cette relation. Les données commerciales sur le C/f n'étaient pas en relation linéaire avec les variations du nombre de femelles, mais il existait une relation asymptotique entre ces valeurs, ce qui révèle que les données C/f sous-estiment les variations en pourcentage de la population d'aloses femelles. La relation inverse entre la capturabilité et le nombre de femelles n'était pas causée par des améliorations périodiques des engins, mais était plutôt due à la capacité des pêcheurs commerciaux d'exploiter par action différentielle les concentrations d'aloses femelles au cours de la montaison.

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Management strategies of American shad stocks, *Alosa sapidissima*, in their natal rivers have traditionally involved fishing effort regulations, including gear restrictions and/or limitations on the number of fishing days per week (Mansueti and Kolb 1953; Walburg and Nichols 1967). Effort regulations can effectively control overfishing provided that the fishing mortality rate (F) is directly proportional to fishing effort (f):

$$F = qf \quad (1)$$

where the catchability coefficient (q), the proportion of the stock removed by one unit of effort, is constant (Gulland 1964; Garrod 1964). If this assumption holds, fishing mortality can be monitored effectively by controlling fishing effort, and stock abundance estimated by changes in catch per unit of effort (C/f). However, the proportionality between F and f often fails due to variations in q resulting from seasonal changes in stock availability, gear selectivity, and gear saturation (Gulland 1964; Garrod 1964; Pope and Garrod 1975). Paloheimo and Dickie (1964) theorized that q should vary inversely with stock abundance (N) according to an inverse power function:

$$q = aN^B \quad (2)$$

where the parameters a and B are constants. This result could be affected by nonrandom search behavior by fishermen coupled with strong schooling behavior (Clark 1974; Rothschild 1977). If q varies inversely with N, constant fishing effort will generate a constant catch rather than a constant fishing mortality rate (Radovich 1976), and C/f will no longer be directly proportional to changes in stock size (Gulland 1977; Radovich 1979). When this occurs, catch and effort data and yield per recruit and surplus production models (Pope and Garrod 1975) will provide misleading information relating to stock status and fishing rates.

Whereas the Paloheimo and Dickie hypothesis has been veri-

fied for certain anadromous and marine fishes (Bannerot and Austin 1983), it has not been examined for American shad. Given the widespread use of commercial catch statistics to assess the status of American shad stocks along the east coast of North America, a rigorous examination of this hypothesis is needed. In this paper, we tested the Paloheimo and Dickie hypothesis for Connecticut River shad using commercial catch and effort data taken from 1970 through 1983, and with relative population estimates from the Holyoke Dam fishlift facility. We also evaluated the functional relationship between commercial C/f and stock size, and analyzed the extent to which density-dependent catchability is promoted by a patchy distribution of the shad runs created by nonrandom commercial fishing practices.

Methods

Data Sources

Commercial fishermen harvest adult American shad in the lower Connecticut River (km 1–35) with multifilament drift gill nets from mid-April through mid-June (Fredin 1954; Jones et al. 1976). Fishing is allowed five nights per week (Sunday through Thursday). Connecticut State statute requires the reporting of daily landings to the Department of Environmental Protection. Landings are believed to be underreported for tax purposes, and because male shad are culled owing to their low market value (Moss 1946; Leggett 1976). Correction factors have now been developed and have been applied to reported landings from 1970 through 1983 (Jones et al. 1976; Crecco et al. 1982). In this paper, corrected landings are used and are referred to as adjusted commercial landings.

Estimates of the number of adult American shad entering the Connecticut River annually from 1966 through 1983 have been made using tag–recapture experiments (Leggett 1976; Minta 1979) and commercial catch and effort data (Crecco et al. 1981, 1982). Both methods have used adjusted commercial landings. The sex ratio, age composition, and incidence of repeat spawning have also been monitored annually from commercial scale samples. These data were biased toward larger (>47 cm fork length, FL) female shad due to gillnet selectivity (Crecco et al. 1981). This bias has been identified and quantified using age and sex ratios from experimental pound nets (Minta 1980) and by determining length-specific fishing rates from the 1974 through 1980 tag–recapture experiments. Because male shad population and age data were severely affected by gillnet selectivity and differential culling, we used only female shad data for these analyses.

Tests of the Paloheimo and Dickie (1964) hypothesis require both commercial catch and effort data and population estimates that are derived independently of the commercial statistics (Ulltang 1976). Relative population estimates independent of commercial statistics were derived from May and June lift data at the Holyoke Dam (river km 128). Daily counts of American shad lifted at the Holyoke lift have been made annually since 1955 (Watson 1970; Moffitt et al. 1981; Krska et al. 1982, 1983). We did not use daily passage data from 1955 through 1961 because it is uncertain whether low passage rates in these years were due to low population size or to the tendency of adult American shad to spawn below the Holyoke Dam during the initial years of fish passage (Carscadden and Leggett 1975).

Major technological improvements in the Holyoke fishlift occurred in 1969, 1975, and 1976 (Henry 1976). These are reflected in a systematic increase in the mean annual passage rate (number of shad per day) during four time periods (1962–68, 1969–74, 1975, 1976–83) after fishlift improvements took place (Table 1). We developed weighting coefficients to reflect the technological changes in the fishlift by dividing the mean annual passage rate from 1962 to 1968 by the mean annual passage rate from 1969 to 1974, 1975, and from 1976 to 1983. The population size of American shad entering the Connecticut River from 1962 to 1983 was estimated by (1) dividing the number of American shad lifted annually by the number of days at which 99% of the fish were passed, (2) multiplying this lift rate by the appropriate weighting coefficient from Table 1, and (3) multiplying the lift rate by 1000 to scale the population estimates to the magnitude of the commercial population estimates. Finally, the annual population of female American shad was estimated (Table 2) by multiplying the total population estimate by that year's sex ratio adjusted for gillnet selectivity (Crecco et al. 1981, 1982).

TABLE 1. Computations to determine weighting coefficients for technical improvements in the Holyoke fishlift in 1969, 1975, and 1976.

Years	No. lifted/day	SD	Lift improvement year[a]	Weighting coefficient[b]
1962–68	871.47	196.40		1.00
1969–74	1319.45	474.66	1969	0.66
1975	3236.69		1975	0.27
1976–83	8665.75	3061.97	1976	0.10

[a]A crowding device was added to the fishlift in 1969. The hopper capacity of the tail race facility was increased from 2508 to 6306 L in 1975. A permanent spillway fishlift was installed in 1976.

[b]Weighting coefficient: 1969–74 = 871.47/1319.45 = 0.66; 1975 = 871.47/3226.69 = 0.27; 1976–83 = 871.47/8665.75 = 0.10.

If the population estimates from the Holyoke lift (Table 2) reflect unbiased changes in the American shad population size, they should satisfy two criteria. Firstly, the overall changes in the Holyoke population estimates should follow a similar trend as the population estimates based on commercial data. Secondly there should be a high positive correlation between year class strength estimates of female American shad from the Holyoke population estimates and the corresponding juvenile indices of abundance from 1967 to 1978. We ran a linear regression analysis between the population estimates from the Holyoke lift and the corresponding commercial population estimates. There was a significant positive correlation ($r = +0.68$, $P < 0.01$) between the two data sets. Next, we related the 1967–78 year class strength estimates of female American shad from the Holyoke lift to the corresponding juvenile indices. Year class strength was the total contribution of virgin female shad of each year class in the 1970–83 populations based on the age structure (Leggett 1976; Jones et al. 1976; Crecco et al. 1983). We found that year class strength estimates from the Holyoke lift data were positively correlated ($r = +0.90$, $P < 0.001$) with the juvenile indices (Table 3). More importantly, the coefficient of variation (cv) among the juvenile indices (cv = 58.3%) was high, and more consistent with the variability in the Holyoke data (cv = 44.9%) than in the commercial data (cv = 31.9%). This indicates that the relative magnitude and variability in the recruitment levels based on the Holyoke lift most likely reflected true changes in American shad year class strength.

TABLE 2. Observed and adjusted lift data (Moffitt et al. 1981; Krska et al. 1982, 1983) of American shad over the Holyoke Dam from 1962 through 1983.

Year	Lift days	No. shad lifted	$\bar{x}$ shad/day	Adj. pop. size[a]	Adj. female pop. size[b]
1962	26	21.282	818.54	818.54	
1963	25	29.418	1176.72	1176.72	
1964	37	34.843	941.70	941.70	
1965	31	33.514	1081.10	1081.10	
1966	29	16.044	553.24	553.24	
1967	26	19.299	742.27	742.27	
1968	31	24.389	786.74	786.74	
1969	28	45.300	1612.61	1064.32	
1970	36	65.075	1807.64	1193.04	466.82
1971	29	52.241	1801.41	1188.93	468.06
1972	34	25.309	744.38	491.29	210.29
1973	39	24.878	637.90	421.01	166.10
1974	40	52.510	1312.75	866.42	351.47
1975	35	112.934	3226.69	871.21	321.17
1976	32	343.533	107.41	1073.54	522.20
1977	51	201.043	3942.02	394.20	236.14
1978	20	142.134	7106.70	710.67	262.94
1979	40	253.126	6328.00	632.82	295.93
1980	49	372.117	7594.22	759.42	398.81
1981	40	377.124	9428.10	942.81	346.80
1982	25	290.163	11606.52	1160.65	550.00
1983	37	524.822	14184.38	1418.44	481.74

[a]Adjusted population was estimated annually as follows: 1962–68 = $\bar{x}$ shad lifted/day times 1000; 1969–74 = $\bar{x}$ shad lifted/day times 0.66 times 1000; 1975 = $\bar{x}$ shad lifted/day times 0.27 times 1000; 1976–83 = $\bar{x}$ shad lifted/day times 0.10 times 1000.

[b]Adjusted female population was estimated by multiplying the total adjusted population size by the female sex ratio determined from commercial data.

TABLE 3. Juvenile relative index of abundance from the 1967–78 year classes and the resulting number of virgin female shad from each year class based on commercial catch and effort data and adjusted Holyoke lift data (b = slope, a = y-axis intercept).

Year class (t)	Juvenile index	Female shad commercial index	Female shad Holyoke index
1967	20.2	209 000	222 000
1968	11.1	164 000	118 000
1969	19.0	248 000	245 000
1970	27.8	293 000	275 000
1971	65.7	459 000	491 000
1972	15.3	270 000	215 000
1973	12.4	168 000	154 000
1974	21.4	304 000	326 000
1975	23.7	261 000	280 000
1976	22.4	275 000	325 000
1977[a]	—	428 000	620 000
1978	27.2	211 000	278 000
$\bar{x}$	24.20	274 000	296 000
SD	14.11	87 366	132 994
N	11	11	11
CV	58.30	31.90	44.90

	Linear regression	
	Juvenile index vs. commercial pop. size	Juvenile index vs. Holyoke pop. size
r	+0.883	+0.898
b	4843.28	5996.51
a	142974.40	1217.21
P	<0.001	<0.001

[a]No juvenile sampling was conducted in 1977.

Catchability Coefficients

Analysis

Commercial q values for female American shad were estimated by rearranging equation (1):

$$(3) \quad q = F/f$$

where f is the fishing effort, defined as the number of gillnet days. The annual fishing mortality rates (F) for a seasonal fishery (Ricker 1975) were derived by dividing the adjusted female catch (C) by the population estimate (N) of female American shad derived from the Holyoke fishlift:

$$(4) \quad F = C/N$$

which, when substituted into equation (3), gave

$$(5) \quad q = C/fN$$

The relationship between q and N from 1970 through 1983 was fitted to a power function:

$$(6) \quad q = aN^B$$

with a nonlinear least square regression (SAS 1982). Bannerot and Austin (1983) showed that, provided the function describes accurately the relationship between q and N, the catch can be expressed by rearranging equation (5) and substituting aN^B for q

$$(7) \quad C = aN^B fN$$

or

$$(8) \quad C = aN^{B+1}f$$

from which C/f is described by

$$(9) \quad C/f = aN^{B+1}.$$

While the nonlinear solution to equation (6) may provide the best predictions of q given population size (Pope and Shanks 1982), it does not furnish the best functional relationship between variables, since both q and N are subject to unknown levels of random variation and measurement errors (Jolicoeur and Heusner 1971; MacCall 1976). The underlying functional relationship between q and N and the best mathematical estimate of the slope (B) was estimated by geometric mean (GM) regression of log q versus log N (Ricker 1973). The standard error of the GM slope (B') was estimated by the method of Jolicoeur and Heusner (1971), and the statistical significance ($P < 0.05$) of B' was tested against the null hypothesis $B' = 0$. If B' is negative and significantly different from 0, the relationship between catchability and female shad population size is inverse. This condition would support the Paloheimo and Dickie (1964) hypothesis.

Results

The commercial q values exhibited no time series trends between 1970 and 1983 (Fig. 1), but showed a significant inverse relationship to female population size (Fig. 2). The inverse

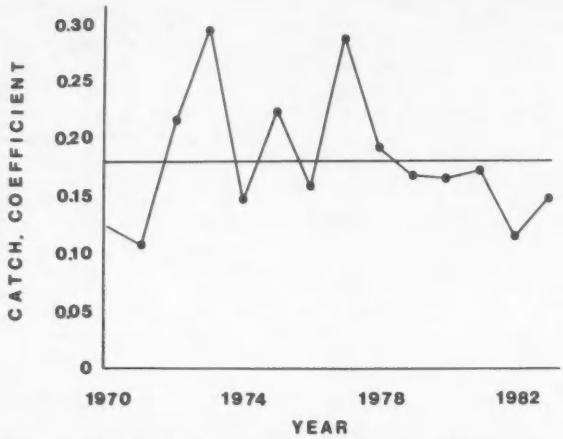

FIG. 1. Adult female American shad commercial catchability coefficients, 1970–83.

power function accounted for 76% of the variation between q and N, indicating a rise in fishing mortality per unit of effort as the population declined. The slopes of the predictive ($B = -0.743$) and GM ($B' = -0.851$) regressions were similar in magnitude, both being significantly ($P < 0.001$) different from 0 (Table 4). These data support the Paloheimo and Dickie hypothesis for Connecticut River shad, and demonstrate the depensatory nature of commercial shad fishing.

Commercial C/f vs. Population Size

Because q values for Connecticut River shad are inversely related to abundance, C/f cannot be a linear function of population size. Instead, C/f should show either no relationship to stock size ($B = -1.0$) or an asymptotic relationship ($0 > B > -1.0$).

Analysis

We examined the functional relationship between commercial C/f and N by fitting these data to linear, power (equation (9)), and asymptotic models:

$$(10) \quad C/f = L - (cd^N)$$

where L = asymptotic C/f and c and d = exponents to be estimated, as recommended by Peterman and Steer (1981). The power and asymptotic models were fitted by the nonlinear least square method, and the exponent of the power function was estimated by GM regression based on log-transformed data. If the c and d exponents of equation (10) differ significantly from 0, C/f is not directly proportional to N. Likewise, the GM slope (B') of equation (9) was tested against the null hypothesis $B' = 0$ (C/f linearly related to N). The hypothesis test $B = 0$ for equation (9) is more valid than that for equation (6), since the variates q (C/fN) and N of equation (6) are not mutually independent.

TABLE 4. Parameter estimates for the nonlinear regression and geometric (GM) functional regressions (r^2 = coefficient of determination).

Parameter	Estimate	SE	r^2	t-statistic $B = 0$	P
		Nonlinear regression			
A	13.136	8.678	0.848		
B	−0.743	0.117		6.0	<0.001
		GM regression			
A'	19.836				
B'	−0.851	0.103		8.262	<0.001

Results

There was a significant ($P < 0.05$) curvilinear relationship between commercial C/f and female population size with both the power (equation (9)) and asymptotic functions (equation (10)) (Fig. 3). The coefficients of determination (r^2) between C/f and N exceeded 0.77 for both models (Table 5). The r^2 for the linear model was 0.262. The null hypothesis of linearity between C/f and N for Connecticut River shad was rejected ($P < 0.01$) by the power and asymptotic models. The asymptotic relationship between commercial C/f and female shad popula-

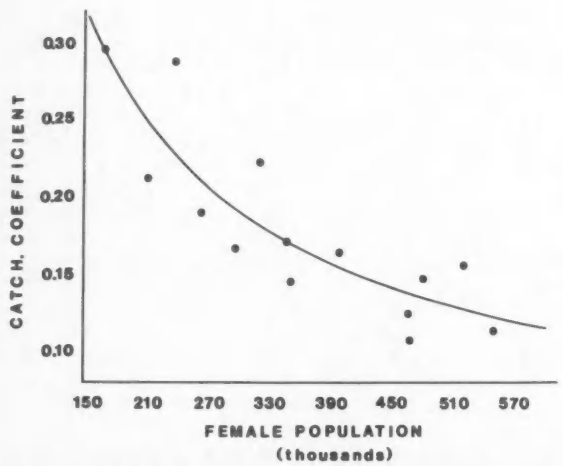

FIG. 2. Relationship between adult female American shad population size and commercial catchability coefficients for these fish.

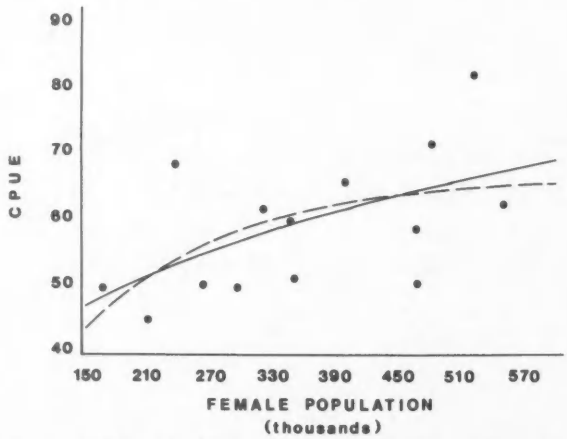

FIG. 3. Relationship between adult female American shad population size and CPUE's. Both power (solid curve) and asymptotic (broken curve) functions are fitted.

TABLE 5. Estimates of exponents of the relationship between commercial catch per effort (C/f) data and female shad population size with nonlinear power, GM power, and asymptotic models (r^2 = coefficient of determination).

Parameter	Estimate	SE	r^2	t-statistic $B = 0$	P
	Power function: $C/f = aN^{(1+B)}$				
A	11.588	8.087	0.788		
B	−0.724	0.118		6.136	<0.001
	GM regression power function: $C/f = aN^{(1+B)}$				
A'	27.190	—		4.584	<0.001
B'	−0.816	0.178			
	Asymptotic function: $C/f = L - (cd^N)$				
L	65.704	6.017	0.744	10.920	<0.001
c	64.944	10.361		6.268	<0.001
d	0.993	0.0025		397.20	<0.001

tion size displayed the weakness of using commercial data to monitor stock changes. Using our estimates of a and B (Table 4), the annual fishing rate (F) is estimated by substituting aN^B for q in equation (1):

(11) $F = aN^Bf$

from which the catch (C) is estimated by

(12) $C = FN$.

At a fishing effort (f) of 1000 units and a population size (N) of 400 000 female shad, the annual fishing rate is 15.3% and the catch is 61 200 female shad. If N is reduced to 100 000 female shad at a constant fishing effort (1000), F would rise dramatically to 42.9%, resulting in a catch of 42 900 female shad. Thus, a fourfold decrease in female population size (400 000 to 100 000) gives rise to only a 1.4-fold decrement in C/f (61 200 to 42 900), demonstrating that commercial C/f data for female American shad seriously underestimates the percent decline in female stock size when the exponent B is −0.743.

Temporal Heterogeneity and Marked Fish

Paloheimo and Dickie (1964) showed that the inverse relationship between q and fish abundance can result from spatial patchiness of the fish population relative to the area being fished, and from the tendency of fishermen to differentially locate and exploit these patches. If the temporal distribution of American shad entering the Connecticut River is patchy, the frequency distribution of daily female shad C/f should follow the negative binomial or some other contagious distribution (Evans 1953).

Fish Patchiness

Analysis

We fitted the daily female shad C/f (catch per gillnet haul) from 1978 to 1980 tagging studies (Minta 1980) to the negative binomial and Neyman type A distributions with the T and U statistics for observed and expected moments (Elliot 1971). If the distribution of daily female shad C/f data conforms to either the negative binomial or the Neyman type A models, the estimated T and U statistics should be significantly ($P < 0.05$) less than twice their standard errors. During all tagging experiments, the number of female shad taken in each drift and the drift time (minutes) were recorded daily. Later, the catch per drift was adjusted to a constant drift time (20 min). This made the daily C/f data more proportional to daily changes in female shad relative abundance. Daily shad C/f data from 1981 to 1983 could not be analyzed because tagging experiments were abandoned after 1980.

Results

The frequency distributions of daily female shad catches per gillnet haul from 1978 to 1980 were markedly skewed to the right (Fig. 4). The variance-to-mean ratios were always significantly ($P < 0.05$) greater than 1:1, indicating the temporal patchiness of female shad gillnet catches at the river mouth (Table 6). The daily frequencies of shad C/f from 1978 to 1980 were also consistent with the negative binomial and Neyman type A distributions, although the less skewed Neyman type A

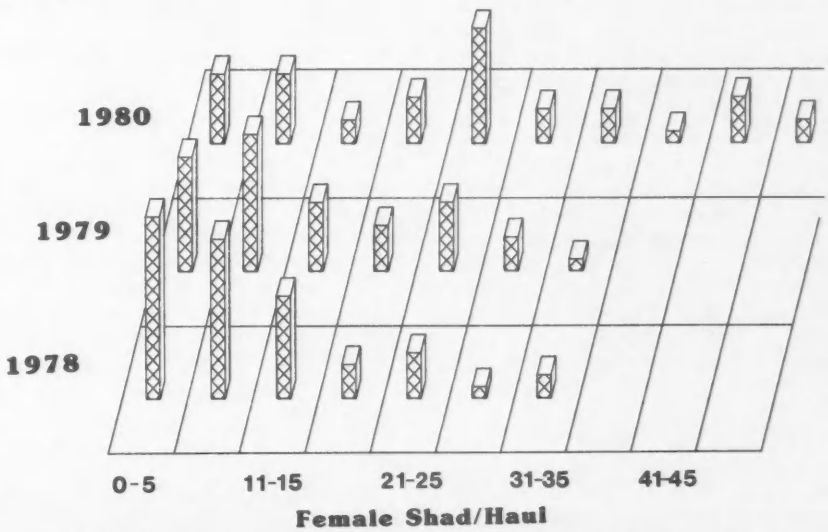

FIG. 4. Frequency distributions of daily female shad catches per gillnet haul, 1978–80.

TABLE 6. Fit of the Neyman type A and negative binomial distributions to daily net C/f data from 1978 to 1981 (N = number of daily samples, K = coefficient of aggregation, U = difference between observed and expected variance, T = difference between observed and expected third moment, $U = 0$ or $T = 0$).

	1978	1979	1980
	Neyman type A		
Mean C/f	8.93	11.71	21.75
s^2	70.64	65.97	191.34
K	1.27	2.50	2.76
N	49	42	41
U-value	1.11	−0.600	−1.809
SE U	10.01	12.34	30.21
t	0.11	−0.05	−0.06
P	<0.90	<0.90	<0.90
	Negative binomial		
T-value	−2645.93	−478.18	31.56
SE	1483.65	501.49	8.57
t	−1.78	−0.954	−0.877
P	0.10	0.40	0.40

was a much better fit to the three distributions. The contagious distribution of daily shad C/f data provides convincing evidence that female American shad are distributed in patches during their upriver migration.

Nonrandom Fishing Effort

Analysis

If commercial fishermen nonrandomly exploit patches of adult shad entering the river, there should be a positive linear or nonlinear relationship between commercial fishing effort and shad relative abundance. We assessed these predictions using weekly mean female shad catch per gillnet haul from the 1978–80 tagging experiments as a weekly index of stock abundance. Weekly mean fishing effort (h) data for 1978–80 were developed from daily effort records submitted by nine commercial fishermen known to be reliable. Linear and nonlinear regression analyses were conducted to determine the shape of the short-term numerical response (Hassell 1978) between weekly changes in fishing effort and relative abundance entering the river from 1978 to 1980.

Results

The weekly fishing effort (h) expended by nine commercial fishermen from 1978 to 1980 followed a sigmoid relationship with weekly changes in female shad relative abundance (Fig. 5). A logistic model described more than 80% of the variation. The approach of commerical fishing effort to an asymptote at the peak of the shad run is realistic, given that the weekly magnitude of commercial shad fishing is limited by law to five nights. These data strongly suggest that commercial shad fishermen fish nonrandomly, exerting more fishing effort during the peaks of the annual shad migration.

Effects of Fishing Effort and Gear Saturation

An inverse power function between q and N could also be induced by numerical responses, gear saturation, and/or cooperation among fishermen (Rothschild 1977; Peterman and Steer 1981).

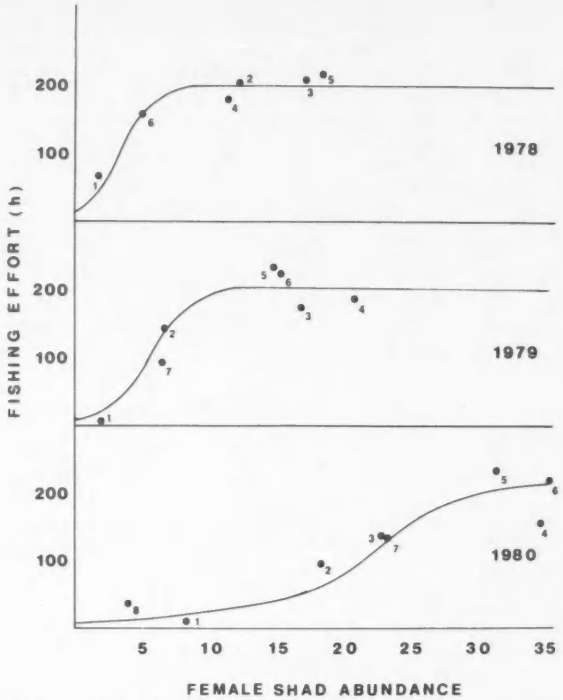

FIG. 5. Weekly changes in commercial fishing effort vs. weekly changes in female shad relative abundance per gillnet haul in 1978, 1979, and 1980. Numbers indicate consecutive 7-d periods from April 1 to May 30.

Analysis

The effects of numerical responses (the ways in which fishing effort changes annually with population size) were assessed by plotting commercial fishing effort against both current and the previous year's female population size and commercial C/f. A significant ($P < 0.05$) linear or nonlinear relationship between effort and abundance would suggest that numerical responses affect the relationship between q and N. The effects of gear saturation were evaluated by plotting the annual commercial fishing rate (F) against fishing effort (Rothschild 1977) from 1970 to 1983. An asymptotic fit would suggest gear saturation.

Results

There were no significant ($P < 0.25$) linear or nonlinear relationships between fishing effort and current or lagged population size and C/f. Numerical responses between fishing effort and female shad population abundance are therefore weak. Annual changes in fishing effort can thus be viewed as a random variable, having little influence on q. The relationship between F and fishing effort was linear (Fig. 6), so there was no evidence that the inverse relationship between q and N could be ascribed to gear saturation.

Discussion

Implications of Variable q on Fishing Theory

The traditional theory of fishing (Baranov 1918; Beverton and Holt 1957) states that percent changes in fishing mortality are directly proportional to percent changes in fishing effort, and

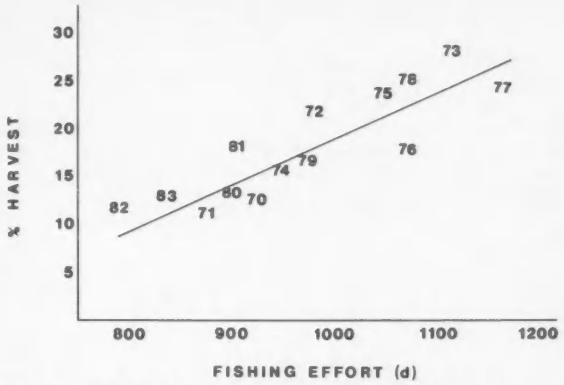

FIG. 6. Relationship between percent harvest and changes in commercial fishing effort from 1970 through 1983.

that C/f data are linearly related to changes in stock size. This theory depends on the underlying assumption that q is constant, or at least independent of stock size, so that the exponent B of the power function approaches zero. This theory has been widely accepted in fish population studies (Ricker 1975), and has served as a rationale behind management strategies such as effort control and limited entry (Ulltang 1980; Pope 1980). Paloheimo and Dickie (1964) challenged the assumption of constant q, arguing that q is inversely related to stock size due to spatial heterogeneity of the fish stock and nonrandom search behavior of fishermen. Our findings for the Connecticut River commercial shad fishery are consistent with the Paloheimo and Dickie hypothesis. This indicates that in this population, and undoubtedly in other exploited shad populations, fishing mortality rates would rise steadily as the female shad run is depleted, even if fishing effort is held constant. Whereas the degree of bias associated with the exponent B can be used to adjust C/f data (Bannerot and Austin 1983), valid estimates of B require relative population estimates that are derived independently of commercial data. Such independent estimates are not generally available for other shad populations (Walburg and Nichols 1967; Leggett 1976).

Management Implications

The negative feedback between shad abundance and commercial catchability can be considered a depensatory mortality factor (Clark 1974; Peterman 1977). Our data indicate that any given increase in fishing effort would lead to a much greater rise in the F and a concomitant reduction in shad parent stock size. This would eventually cause recruitment failure unless fishing effort was reduced drastically at the first signs of stock collapse (Fox 1974). The inverse density-dependent nature of q makes it very difficult to minimize recruitment overfishing because the levels of fishing effort at which recruitment failure occurs are difficult to measure with certainty due to climate-induced fluctuations in American shad recruitment at all parent stock sizes (Crecco et al. 1983; Crecco and Savoy 1984). Fishery managers have traditionally been slow to react to signs of recruitment failure because the emergence of two or three weak year classes in the fishery is generally not regarded as convincing evidence of overfishing (Radovich 1979; Pope 1980), as was the case in certain herring stocks (Murphy 1966; Clark 1974).

The inverse relationship between q and fish population size not only reduces the accuracy of C/f data, but also the usefulness of various stock assessment techniques and management options. Valid estimates of natural mortality rates derived from linear regression of total mortality rates on fishing effort depend mainly on the assumption of a constant catchability (Pope 1980), as do population estimates derived by the DeLury method (Ricker 1975). Furthermore, if the exponent is negative, the shape of the yield curves and the F at MSY from dynamic pool (Gulland 1977) and surplus production models (Fox 1974; Radovich 1979) may be misleading at high levels of fishing effort. Pope and Garrod (1975) have also noted that the effectiveness of management strategies such as effort control and limited entry depends greatly on the sign of the exponent B. If $B \geq 0$, effort reduction and limited entry are effective means to control overharvest. When $B < 0$, values of F are no longer proportional to changes in fishing effort. In this case when the stock is severely depleted, a small to moderate reduction in fishing effort may have no effect on the levels of F.

Causes of Variability in q

An inverse relationship between q and N was once thought to be characteristic of fisheries for schooling pelagic fishes (Fox 1974; Schaaf 1975; Ulltang 1976; MacCall 1976). This phenomenon now appears to be widespread and also applicable to anadromous (Peterman et al. 1979; Peterman 1980; Peterman and Steer 1981), demersal marine (Pope and Garrod 1975; Garrod 1977; Houghton and Flatman 1980; Bannerot and Austin 1983), and freshwater fishes (Henderson et al. 1983).

The causes of an inverse relationship between q and N have often been attributed to temporal improvements in fishing power (Gulland 1964), numerical responses (Rothschild 1977), gear saturation (Garrod 1964), schooling behavior of the fish stock, and nonrandom search behavior by fishermen (Paloheimo and Dickie 1964). There is no evidence that the inverse density-dependent q was due to recent improvements in gear or vessel performance from 1970 to 1983 (Fig. 2). The commercial shad fishery in the Connecticut River has used only multifilament drift gill nets and small boats to harvest shad during the last 20 yr (Walburg and Nichols 1967; Leggett 1976).

Similarly, there was no evidence of a significant numerical response between annual changes in commercial fishing effort and current or lagged female shad population size. The weekly fishing effort did, however, increase in a sigmoid pattern with female shad population size (Fig. 6–8), indicating that commercial shad fishermen concentrate their effort nonrandomly during the peak of the shad migration. The nonrandom search behavior of shad fishermen is consistent with the Paloheimo and Dickie hypothesis. Such behavior appears to be characteristic of other anadromous commercial fisheries (Peterman et al. 1979).

Fish commonly exhibit schooling behavior, as indicated by the high variance to mean ratios among various sampling surveys (Taylor 1953; Grosselein 1971; Jones and Pope 1973). American shad likewise show strong schooling behavior during their upriver migration. Our high variance to mean ratios and skewed frequency distribution of daily gillnet catches from 1978 through 1980 (Table 7) indicated that the temporal distribution of shad gillnet catches was heterogeneous and most consistent with a Neyman type A distribution, suggesting that patches of American shad randomly enter the river (Elliot 1971). Whereas direct evidence on the spatial heterogeneity of the shad runs is unavailable, commercial shad catches are known to vary greatly along the river during the same week

(Fredin 1954; Crecco et al. 1982). This implies that the shad run is also spatially heterogeneous.

Shad Fishermen as Predators

Holling (1965) found that the functional response of vertebrate and invertebrate predators could be classified as linear (type I), asymptotic (type II), or sigmoid (type III). He reported that an asymptotic functional response at high prey density is due to increased prey handling time at the expense of search time. If the commercial shad fishery is viewed as a predator–prey system, one reason for our asymptotic functional response may be that fishing time declines at high shad abundance because fishermen spend more time emptying and resetting their nets. Differential handling time is particularly relevant to commercial gillnet fisheries on the Atlantic coast, since shad fishermen are typically allowed to harvest shad on a restricted number of days per week, and the multifilament nets used further limit shad fishing to early freshet periods, cloudy days, and at night.

The nonrandom search behavior of commercial shad fishermen is partly due to their prior knowledge of American shad migratory patterns (Leggett 1976; Crecco et al. 1982). Shad fishermen know that the shad migration in the Connecticut River begins when water temperatures reach about 8°C (Leggett and Whitney 1972; Leggett 1977). They are also aware that female American shad enter the river later than male shad, and they use large-mesh nets to selectively harvest the more valuable female shad (Fredin 1954; Leggett 1976). They also know that shad ascend the river from the channel side (Leggett 1976) and thus drift their gill nets through deep water. Clearly, commercial shad fishermen do not search randomly. Instead they fish where and when the probability of catching female shad is greatest.

The nonrandom search pattern of commercial fishermen is also influenced by catch information received from other fishermen. Groups of shad fishermen are known to set their gill nets at particular access points (reaches) along the lower river (Fredin 1954). When a fisherman at a certain reach catches large numbers of shad at an ebb tide, this information eventually spreads to the other fishermen within that reach. They are apt to initiate their search at the same tide during subsequent days when the probability of successive good catches is high. Conversely, a poor catch from a particular reach might prompt other fishermen to search during other tidal conditions, thereby enhancing their chances of success.

We conclude that the inverse relationship between q and N demonstrated for female American shad in the Connecticut River is attributed to the ability of commercial fishermen to differentially exploit nonrandomly distributed schools. This indicates that q is more sensitive to the number of shad within a school than to the total population size (Paloheimo and Dickie 1964; Radovich 1976). During years of low stock size, commercial fishermen use their prior experience to concentrate their effort on temporally and spatially localized shad. This yields higher values of q at low stock size. Only in the unlikely case in which changes in shad population size are directly proportional to changes in the number of shad per school does q remain constant. Because the search pattern among commercial fishermen departs from a random process, any attempt to model this fishery should incorporate the effects of schooling behavior of shad and the nonrandom search behavior of fishermen.

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Role of Olfaction in the Behavioral and Neuronal Responses of Atlantic Salmon, *Salmo salar*, to Hydrographic Stratification[1]

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The behavior of sham-operated and anosmic Atlantic salmon, *Salmo salar*, was studied in a fjord system with close reference to the fine-scale hydrographic features. Control fish made small-amplitude vertical movements, with sudden large-amplitude excursions. The anosmic fish made large continuous searches up and down in the water column, descended below the sill depth of the fjord, and followed the bottom contours. None of these three behaviors was seen in the control fish. The trauma caused by the surgical incision did not prevent the fish from active swimming, and a fish with unilateral sectioning of the olfactory nerve returned to the river of release. Activity of single olfactory bulb neurons was recorded during stimulation of salmon olfactory epithelium with water samples taken from different depths of the fjord. These water samples had been taken from regions that showed layering and to which migrating salmon demonstrated behavioral preferences in ultrasonic tracking experiments. Ninety percent of responding neurons showed differencial responses to the water samples, indicating the capacity of the olfactory system to discriminate among stratified water layers found in the ocean. We conclude that olfactory discrimination of fine-scale hydrographic features may provide a necessary reference system for successful orientation in nearshore regions by salmon.

Le comportement de saumons atlantiques (*Salmo salar*) anosmiques et faisant l'objet d'expériences à blanc a été étudié dans un fjord par rapport aux microstructures hydrographiques. Les poissons témoins ont effectué des migrations verticales de faible amplitude accompagnées de déplacements soudains de grande amplitude, tandis que les poissons anosmiques ont effectué des mouvements ininterrompus de montée et de descente, sont descendus plus bas que le seuil du fjord et ont suivi les contours du fond. Aucun de ces comportements n'a été observé chez les poissons témoins. Le trauma causé par l'incision chirurgicale n'a pas empêché le poissons de nager activement; un poisson dont le nerf olfactif avait été sectionné unilatéralement est retourné à la rivière où il avait été relâché. On a noté l'activité de neurones individuels du bulbe olfactif pendant la stimulation de l'épithélium olfactif du saumon avec des échantillons d'eau recueillis à différentes profondeurs du fjord, à des endroits qui montraient une disposition en couches où les saumons migrateurs manifestaient des préférences comportementales au cours d'expériences de dépistage ultrasoniques. Chez 90 % des neurones réactifs, on a noté des réactions différentielles aux échantillons d'eau, ce qui porte à croire que le système olfactif peut distinguer les différentes couches océaniques stratifiées. Les auteurs formulent la conclusion que la discrimination olfactive de microstructure hydrographiques peut représenter un système de repère nécessaire à l'orientation adéquate du saumon dans les régions côtières.

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The migration of salmon from the oceanic feeding grounds to the homestream spawning site involves orientation in open ocean, coastal waters, and streams. Traditionally the oceanic and stream phases of the migration have been thought to involve different cues and mechanisms (Hasler and Scholz 1983). Sensory impairment studies, demonstrating the requirements of a functioning olfactory system for successful homing in the freshwater phase, have been conducted for many species of salmonids (*Oncorhynchus kisutch*, Wisby and Hasler 1954; *O. nerka*, Lorz and Northcote 1965; *O. keta*, Hiyama et al. 1966; *O. tshawytscha*, Groves et al. 1968 and DeLacy et al.

[1]Dedicated to Professor Arthur D. Hasler in recognition of his many contributions to the study of salmon orientation.

1969; *Salmo clarki*, Jahn 1969; and *S. trutta*, Shearer 1959). Mechanisms of open ocean migration are less well understood although a variety of cues has been suggested (see Brannon 1982 for review).

In the nearshore or coastal zone a variety of cues of both open ocean and stream phases may be used by salmon (Nordeng 1977). In studying the stream phase of homing, Hasler and his co-workers have demonstrated that coho salmon (*O. kisutch*) are attracted by chemical cues (Scholz et al. 1976) and that these cues are used in the upstream migration (Johnsen and Hasler 1980). In the stream phase of the migration, the salmon makes a selection between water masses by horizontal zigzag movements (Johnsen and Hasler 1980; Johnsen 1982). In coastal and oceanic regions the salmon has another degree of freedom and vertical movement becomes an important parameter in behavioral studies. Westerberg (1982), in ultrasonic tracking studies with depth-sensing transmitters, has shown that the salmon's movement is closely related to the fine-scale vertical layering of the water. These observations have led to the suggestion that vertically stratified hydrographic features may be important for the salmon's orienting movements (Westerberg 1984).

In a single ablation experiment, it was observed that an anosmic salmon did not respond to the hydrographic features as did intact fish in the same study (Westerberg 1982). This observation, and the experiments of Craigie (1926) and Bertmar and Toft (1969), which found that fish released in coastal waters without a sense of olfaction did not enter the homestream as well as controls, suggests that olfaction may be as important in coastal, nearshore migrations as in the stream phase of homing.

In the present study we have extended the observations of Westerberg (1982) to a fjord system to confirm that the behavior of salmon in relation to hydrographic stratification is dependent upon an intact olfactory system. We believe we have achieved this by observing the differences between salmon with intact and those with severed olfactory organs. In conjunction with the behavioral observations we conducted electrophysiological studies that demonstrate that single neurons in the salmon olfactory system can discriminate the chemical qualities of the water layers. The available evidence allows us to propose a hypothesis for salmon orientation with respect to the hydrographic stratification in a fjord system.

Methods

Tracking Experiments

The salmon used in our study (Table 1) were mature adults of Imsa River stock, except fish H, which was of the Sandvik River stock of eastern Norway. It was, however, reared from the egg stage in Imsa River water and was released as a 2+ fish in May of 1982 with fish E and F. All fish were captured by salmon trap nets in the fjord near the Imsa River or in a fish trap at the river mouth. Home identity was established by tags and marks. Fish H did return to Imsa River following the experiment.

The experiments were made in the Stavanger fjord system, east and southeast of Stavanger City, southwestern Norway. The interconnected fjords have a total length of more than 100 km, a characteristic width of 3 km, and depth of some 200–300 m. Several sounds, most of them shallow, connect the fjords to the open sea. The deepest sill depth is 56 m. Hydrographically the upper layer of the fjord is strongly stratified, approximately down to the sill depth. The large depth and the small tidal amplitudes make the barotropic currents insignificant, of the order of 0.1 cm/s. The currents in the upper layer of the fjord are mainly wind-driven and transient, superimposed on a weak estuarine circulation. The basin below the sill depth is nearly stagnant. All salmon were released at a common point 8 km from the Imsa River estuary towards the mouth of the fjord. The depth at this location was about 100 m.

TABLE 1. Salmon tracked in the fjord near Ims, Norway, in September 1983. Only fish H was recaptured in the fish trap of the Imsa River.

Fish	Length (cm)	Date (September)	Treatment
C	83	2–3	Intact
D	80	3–4	Anosmic
E	60	4–5	Anosmic
F	66	5–6	Sham
H	72	7–8	Unilateral ablation

Fish that were part of the ablation experiment were anesthetized with chlorobutanol and allowed to recover in a 2-m^3 transport tank at least 6 h before release. Experimental fish (D and E) were rendered anosmic by transection of the olfactory nerve midway between the eyes and the nares. The sham operation (F) was made by a transverse cut through the skin only. The unilateral ablation sham (H) was made by severing the right olfactory nerve and making a sham cut on the left side. The success of this treatment was confirmed by postmortem verification following recapture of fish H in Imsa River on 31 October 1983.

At the time of release the salmon were fitted with sonic tags. Each salmon was held underwater in the tank, in a fish-carrying bag, and the transmitter was inserted into the stomach via the esophagus using a smooth probe. The salmon was then transferred to the sea and gently released at the surface. It is difficult to assess the degree of tagging and handling stress. The first 2 h of each track have been excluded from the data, as in several cases the salmon behaved differently during this period than during the remaining period of tracking. Two of the ablated fish dived to the bottom and stayed there for about 20 min. Most of the salmon swam at above average speed for the first hour after release.

The pressure-sensitive ultrasonic transmitter was 60 mm long, 15 mm in diameter, and weighed 9.5 g in water, or approximately 0.2% of the weight of the salmon. It operated at 49.5 kHz producing a 30-ms pulse with a pulse repetition period varying from 0.5 to 1.5 s over the full pressure range. Each transmitter was calibrated in the sea immediately before tracking by lowering the transmitter attached to the hydrographic sounding instrument. In this way the calibration was made relative to the same depth scale as was used for the hydrographic measurements. The uncertainty in comparing swimming depth and depth of hydrographic features is ±0.2 m. Details of the transmitter, calibration procedure, and data analysis can be found in Westerberg (1983).

Tracking was done from the 31-m research vessel *Svanic* of the University of Gothenburg, Sweden. Positions were obtained by radar ranging of the distances to the shores, with an uncertainty of approximately 50 m. The ship's sonar (Simrad SJ 3) was used in the passive mode as the tracking receiver. The audio signals from the sonar was recorded continuously on a Sony TCD-5 tape recorder for later analyses. During the tracking an online plot of the fish's swimming depth was displayed on a

Hewlett-Packard 85 computer which was connected to a timer/counter (Hewlett-Packard 5316 A) to measure the pulse periods. This information was used to plan the hydrographic sampling. The same equipment was used for the later decoding of the audio tapes. Each pulse period was measured and converted to a depth value. Swimming depths were then averaged over successive 10-s intervals, giving 360 data points per hour of tracking. Those time series were used for the time–depth plots. The relative resolution of the data is approximately 0.2 m.

The physical characteristics of the water were measured with a Neil-Brown Mark IIIb CTD (conductivity–temperature–depth recorder). Given the moderate wave motions in the inshore area of the experiment, the vertical resolution of the CTD was of the order of 0.1 m, enough to resolve the fine-structure features of the stratification. The data were stored in digital form for later analysis.

Electrophysiology

The fish used in these experiments were from the same stock as those used in the tracking studies. Postsmolts (2+ yr) were transported in September 1983 from Ims to the aquarium facility of the Department of Biology, University of Oslo, where they were maintained in freshwater until the end of the experimental studies in January 1984.

Nineteen fish (22–27 cm and 90–190 g) were initially anesthetized with MS-222 (tricain methyl sulfonate), immobilized with Pavulon (3 mg/kg), and placed in an experimental fish holder. The gills of the fish were perfused with water (1 L/min) and anesthesia was maintained during the surgical procedure with MS-222 added to the perfusing water.

To expose the olfactory bulbs, the brain case was opened and the mesenchymal tissue removed. Electrical activity from single neurons was recorded by saline-filled glass microelectrodes (Døving et al. 1974). Most recordings were made from the medial part of the bulb as shown in Fig. 1B. The electrode was positioned using an origin chosen along the midline and at the intersection between the bulbs and the telencephalon. The medial part of the bulb was preferred because previous experiments (Thommesen 1978; Døving et al. 1980) have shown that this part of the salmonid olfactory bulb responds to bile, bile salts, and rinses of conspecifics which would be of interest in the present study. The recording depth varied; most units were obtained between 400 and 900 μm from the surface (Fig. 1A). Electrical signals were amplified by a WPI DAM-5 preamplifier and displayed on a storage oscilloscope screen. Neural activity and an event mark to note stimulation were recorded on a Tandberg FM tape recorder (Series 100, DC to 1250 Hz). Spike activity was later passed through a window discriminator which generated standardized pulses, which were counted by a microcomputer (Mostec Z80) in 1-s time bins. The latter counts for the three trials of each stimulus were added and spike count histograms with 1-s time bins were prepared. Responses were then categorized as facilitated (+), inhibited (−), or unaffected (0) during the experiments and judged again by visual inspection of printouts of the spike count histograms.

Responses to the complete stimulation series with three replicates of each sample were recorded for 43 cells of 19 fish. Of these, 29 cells from 18 fish showed no response to the blank samples of artificial seawater and are included in this study.

Stimulus samples were obtained using a rosette sampler (General Oceanics, Inc.) in conjunction with the CTD. Before sampling, the plastic Niskin bottles were thoroughly rinsed with ethanol and distilled water. The water samples were stored in plastic bottles at 15°C. Two water sample series were collected in the fjord system east of Stavanger, southwestern Norway. Series I (see Table 3) was collected in Høgsfjord (58°54.4′N; 5°59.0′E) near the mouth of Imsa River and series II (see Table 4; Fig. 7) in Fognafjord (59°7.1′N; 5°56.0′E). The sample depths (see Tables 3 and 4) were chosen to represent quasi-homogeneous layers as determined from the CTD plots. For series II they include layers that were occupied by the tracked salmon C for extended periods of time as well as layers that were not selected for appreciable periods. Series II water samples were taken at depths indicated on the temperature and salinity profiles of Fig. 7.

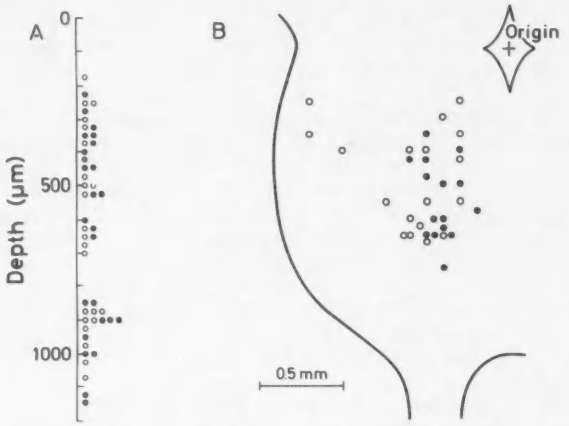

FIG. 1. (A) Recording depths for series I cells (open circles) and series II cells (solid circles); (B) dorsal view of the right olfactory bulb, caudal direction up. The origin is on the midline between the intersection of the bulbs and the telencephalon. Open circles indicate position of the electrode trajectories used to locate cells in series I, and solid circles are for cells in series II.

Artificial seawater (Barnes 1954) was passed through the olfactory organ via the anterior nares. Stimulation with the water samples was made by letting the contents of a 10-mL plastic syringe, one for each sample, flow through the stimulating tube via a three-way stopcock. The samples were presented in three consecutive and equal volumes. The mean flow of water through the olfactory organ was 12 mL/min. No attempt was made to standardize the salinity of the test samples.

Results

Tracking Experiments

Three main observations were made during these trackings. Firstly, depth selection, in the sense that the fish spent prolonged or repeated periods of time in a specific narrow depth interval apart from the surface, was demonstrated only by fish with a functional olfactory system. Secondly, deep dives penetrating into the stagnant basin below the sill depth of the fjord was observed only for the anosmic fish. Thirdly, only the anosmic fish had swimming profiles, suggesting that they followed the bottom.

The main features of the horizontal tracks are summarized in Table 2. The salmon were all released 8 km north of the Imsa River estuary towards the mouth of the fjord. The fjord depth at this location was about 100 m. The movement patterns were

unpredictable. Much of the observed active and directed movements were to the north, away from the Imsa River. All fishes showed periods of active movement both towards north and south. During active periods the movements were essentially along the fjord axis and at a large distance from the shores. Inactive fish often stayed near the shore. A measure of the degree of active horizontal swimming is given in Table 2 by the proportion of time the ground speed averaged higher than 0.15 m/s. This speed is chosen as a rough estimate of a likely maximum current advection velocity.

The time–depth diagrams for the entire trackings are shown in Fig. 2, 3, and 4, in which the time and depth scales are the same for all experiments to facilitate comparison.

Salmon with Intact Olfactory Sense

The vertical tracks of salmon C and F (Fig. 2 and 4) both show characteristics that are similar to earlier trackings of intact salmon, regarding behavior in relation to hydrographic fine-structure (Westerberg 1982). During the first 12 h, salmon C moved steadily towards the outer region of the fjord. Most of this time the salmon followed the interface between a thin brackish layer at the surface and the saltier, cooler water below. In Fig. 5 this is shown in detail in relation to the thermal stratification along the track for a period while the CTD was cycled continuously and the ship slowly followed the fish (a tow-yo). The small-amplitude, vertical zigzag motion was almost continuous and is typical for salmon moving in a fine-structure gradient layer. Salmon F showed a similar behavior while it was swimming at a weak salinity gradient at approximately 4 m (Fig. 6).

At about 06:00, salmon C entered another branch of the fjord system. A turn was made between 10:00 and 12:00. From 12:00 to the termination of the tracking the salmon headed back out from that branch. During this time the fish showed large-amplitude diving activity, with frequent switching between two or more swimming levels, at least some of which can be identified with the fine-structure gradient layers in the CTD recordings (Fig. 7). Salmon F initially headed south into the fjord. After 21:00 the salmon turned north and moved towards the outer part of the fjord until approximately 08:00, after which it stayed passively in a small bay. At the time of the turn, there was, as for salmon C, an increase in swimming activity. An expanded portion of the vertical track for this period is shown in Fig. 6.

Anosmic Salmon

The anosmic salmon D and E both showed a very low mean ground speed (Table 2), but were not passive. As can be seen from Fig. 3, salmon E was active in the vertical direction essentially all of the tracking time. Salmon D remained passive, close to the shore, during the time 01:00 to 04:00, but was otherwise moving in the vertical direction. Tracking was then terminated when the salmon dived below the crushing depth of the transmitter. The activity of the anosmic salmon comprised mostly up and down movements with very little net horizontal progression.

The maximum swimming depth during the dives is unknown, as the modulation circuit of the pressure transmitter was saturated at a depth of 75 m. (An attempt was made to increase the depth range for the experiment with fish E, but this instead caused the transmitter to saturate at a depth less that 10 m, explaining the truncated peaks in the swimming depth diagram in Fig. 3.) The range of dives that can be seen in their entire extension is more than 50 m. If this is extrapolated to the end of the trackings, when only the top of the rises are seen, then the maximum depth was well below 100 m.

TABLE 2. Parameters of the horizontal tracks. The trajectory length, ground speed parameters, and straightness index (SI) were calculated excluding the first 2 h of tracking. SI is defined as the distance from the start to the end of the track in percent of the total trajectory length. The ground speeds are average measures over 30-min time intervals.

Fish	Tracking duration (h)	Length (km)	Ground speed (cm/s)		SI (%)
			Maximum	% of time >15 cm/s	
C	25	24.4	63	78	65
D	11	3.3	20	26	15
E	14	5.3	35	25	86
F	22	12.8	56	53	47
H	16	4.5	35	25	39

There are periods in the tracking of anosmic salmon where the fish changed depth very gradually, interrupted by occasional rises. Typically the vertical velocity was about 0.5 m/min and steady for 10–30 min. This kind of behavior was seen for salmon D during the interval 04:30 to 05:40 and for salmon E from 18:00 to 22:40. During the same periods the salmon were moving slowly and close to the shore. As the sides of the fjord are steep, it was not possible to determine the position of the fish accurately enough with respect to the topography to determine how close it was to the bottom, but it seems reasonable to interpret the periods of slowly varying depths as motion along the bottom. After 23:00, salmon E moved out to the central part of the fjord where the depth was 200–250 m. Here the salmon moved at varying depths in the range 40–50 m, with abrupt rises to the surface. This depth range had the strongest vertical temperature gradient, comprising approximately two thirds of the total temperature difference between the surface and the bottom.

Salmon with Unilateral Ablation

Salmon H was the least active of the salmon tracked. During the first 4 h, the salmon moved erratically in and out of minor bays in the vicinity of the point of release. The hourly mean ground speed was approximately 0.2 m/s. During the following 10 h, the salmon stayed at a depth of about 1 m, holding position at the shore with occasional short displacements. There were a number of brief dives down to 10–15 m. Both active swimming and holding occurred mostly at 1–2 m. This shallow depth was inaccessible for accurate measurements with the CTD because of disturbances by the hull of the ship, so it is not possible to compare the swimming depth with the stratification. Salmon H was captured in the Imsa River 55 d after release.

Electrophysiology

Neurons of the Atlantic salmon olfactory bulb exhibited a low spontaneous discharge rate of about 1 Hz under our test conditions. No change in the spontaneous discharge activity was observed for 58% of the sample presentations, while 25% of the presentations caused an increase in neural activity and 16% suppressed discharging rates. An example of changes in neuron discharge rate for cell 7 in series I to the different water samples

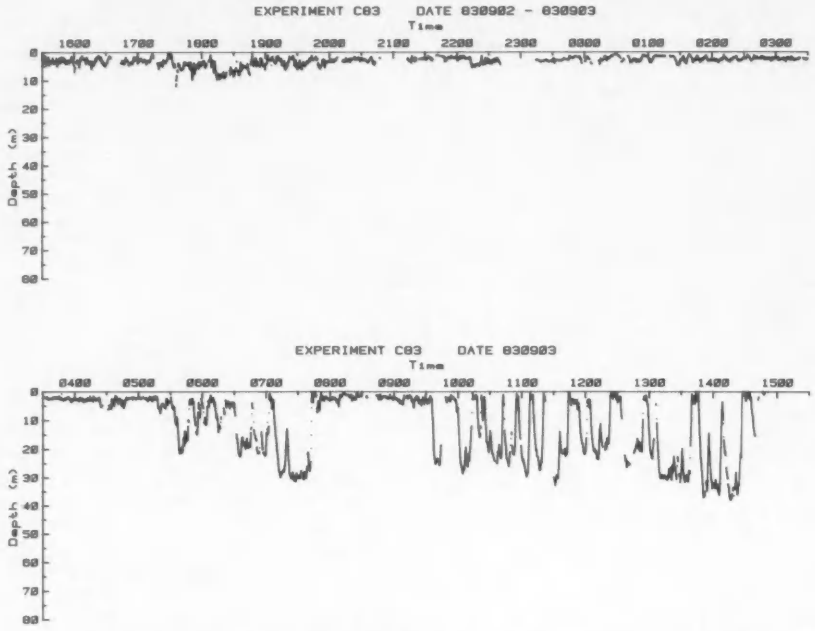

FIG. 2. Time–depth diagram of swimming depth of untreated salmon C. In this and Fig. 3–7 the continuous line shows successive 10-s averages, and the dotted portions indicate periods of low signal-to-noise ratio and data drop-out. Time scale shows local time.

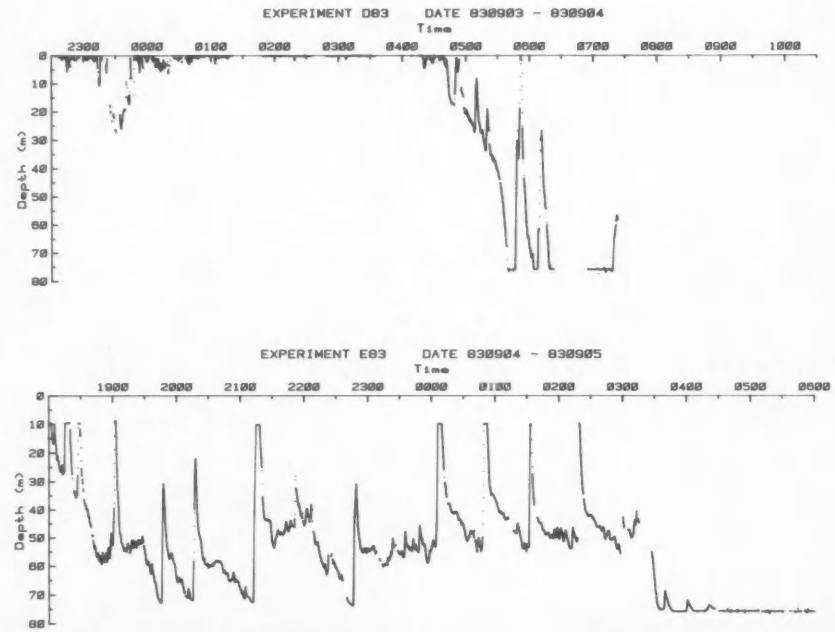

FIG. 3. Swimming depth records of the two anosmic salmon D and E.

FIG. 4. Swimming depth of the sham-operated salmon F and the salmon H with unilateral sectioning of the right olfactory nerve.

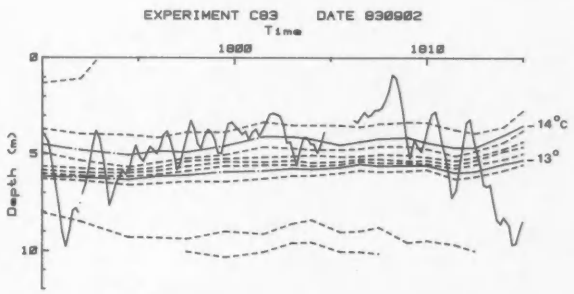

FIG. 5. Detail of the swimming depth of the intact salmon C in relation to the thermal structure along the track. The temperature soundings were made with approximately 2-min intervals, and the isotherms are drawn with a spacing of 0.2°C.

can be seen in Fig. 8. Due to the low discharge rates, interpretation of response category was greatly enhanced by summing the spike counts in each 1-s time bin for the three presentations of each sample. An example of such summed spike count histograms for cell 3 in series II is shown in Fig. 9.

Seventy-two percent of the neurons in this study responded to the test samples. Of the cells responding to the series I water samples, 91% were able to discriminate at least one sample from the others (Table 3), while 90% of the cells responding to series II presentations could discriminate among the water samples (Table 4).

Discussion

We have demonstrated different behaviors betwen intact and anosmic salmon. We have extended the implications of these observations and can report an ability of the salmon olfactory neurons to discriminate water samples taken from different depths during the tracking experiments. From these observations and previous results (Westerberg 1982), we present a hypothesis for salmon orientation in the coastal waters.

Behavior

Fish with intact olfactory systems showed a preference for particular water layers by swimming at those depths for extended periods. These layers are interfaces between quasi-homogeneous layers. The behavior of Atlantic salmon that we observed in the fjord is very similar to that found for Baltic salmon (*Salmo salar*) in the Gulf of Bothnia and landlocked salmon (*S. salar*) in Lake Vänern in Sweden (Westerberg 1982). Typically, the salmon continuously made small-scale vertical movements in the fine-structure gradient layer with occasional larger excursions in the water column. However, these large-amplitude movements were never below the sill depth, marking the separation of the stratified upper layers from the stagnant lower basin.

The behavior of anosmic salmon differed in several aspects. They did not select specific depths and often made larger amplitude movements up and down through the water column. These movements took them much deeper into the fjord, often well into the lower basin. The anosmic fish were also observed to follow bottom contours, unlike the intact fish, which remained in midwater. Behaviors of anosmic fish observed in this study are similar to those described by Westerberg (1982) for an anosmic salmon tracked in Lake Vänern.

Critics of sensory impairment studies (Brett and Groot 1963; Harden-Jones 1968; Peters 1971; Ramsey 1961) have argued that fish suffering these treatments may home with less precision because of generalized traumatic or inhibitory effects rather than loss of the olfactory sense. In spite of the trauma that might have been caused by the ablation procedure of this experiment, our anosmic fish demonstrated large-scale vertical movements,

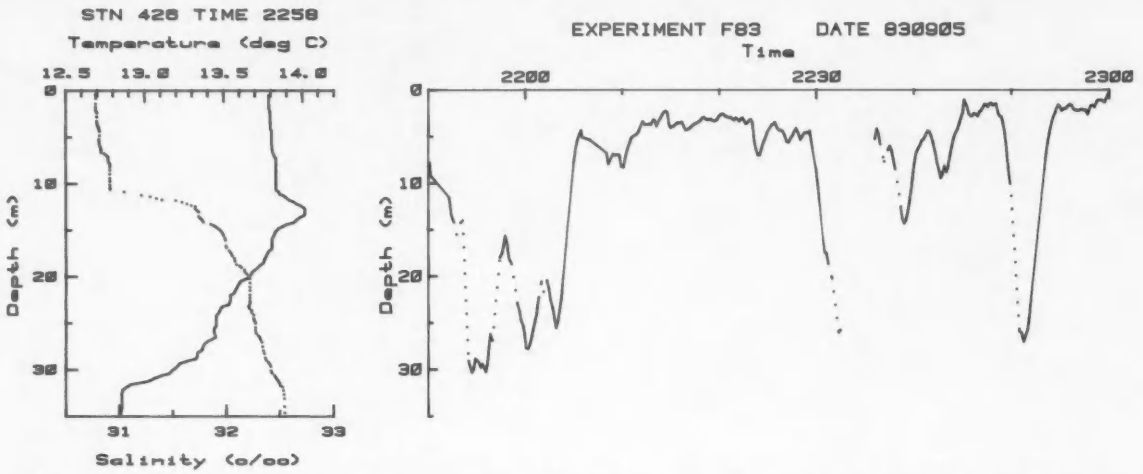

FIG. 6. Swimming depth record of salmon F. A simultaneous CTD recording is shown at left with the depth scale coinciding with that of the swimming depth.

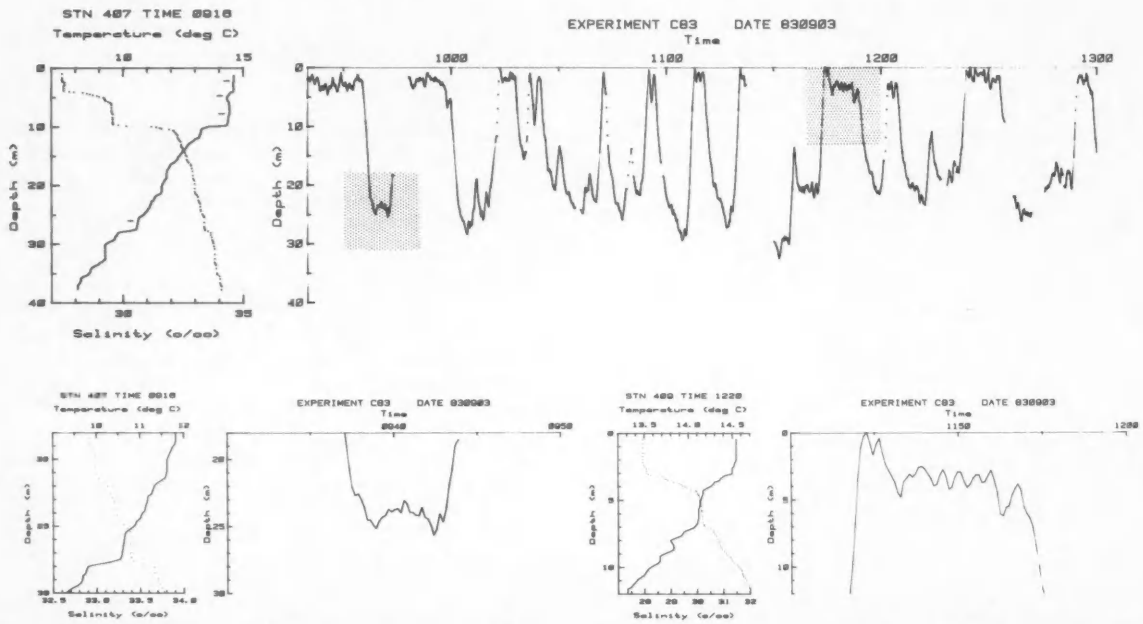

FIG. 7. Swimming depth record of salmon C. Simultaneous temperature and salinity profiles are shown on the left. The shaded parts of the upper diagram are shown expanded in the lower diagrams. The horizontal bars by the upper left temperature profile indicate the depths where water samples for series II were collected.

although the net horizontal progress was slow. Thus the motivation for active swimming seems unaffected by the surgery. We suggest that the large-amplitude swimming behavior of anosmic fish may be described as active, but unsuccessful searches for water layers with suitable odor characteristics. This argument is further supported by the behavior of salmon H, a unilateral ablation, that ultimately entered the river of release.

Physiology

Water samples collected during the tracking studies were used as stimuli for electrophysiological experiments designed to determine if the olfactory system of Atlantic salmon is capable of discriminating fine-structure features of hydrographic stratification. Typically the vertical separation of adjacent samples was 2 m, with temperature and salinity differences of a few tenths of a degree and some parts per thousands, respectively. Sixty-six percent of all olfactory bulb neurons in this study did, in fact, display differential changes in discharge rates in response to test samples. However, only 72% of all neurons included in this study responded to any of the water samples. Of these

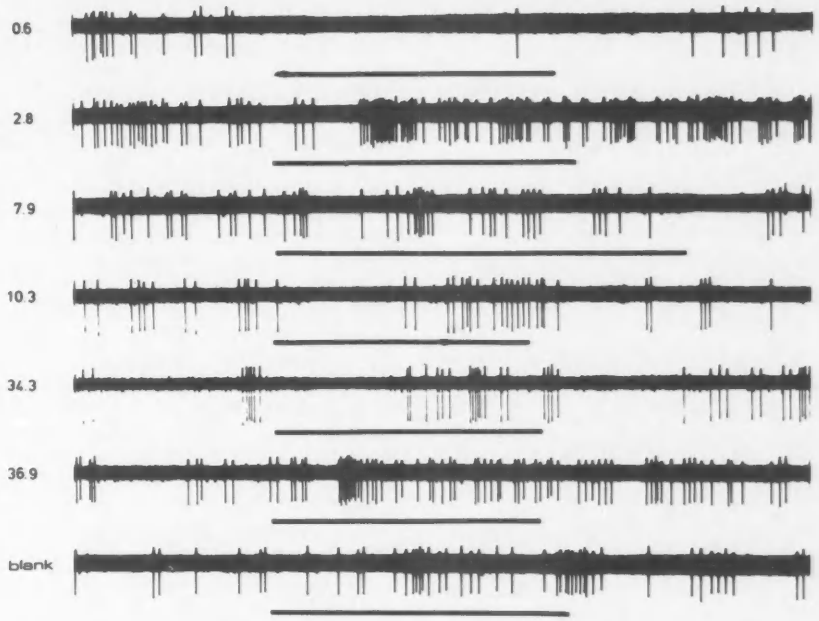

FIG. 8. Responses of a single olfactory bulb neuron in salmon (series I, cell 7) to blank and five water samples. The numbers to the left of each trace indicate the depth in the fjord where the water samples were taken (see also Fig. 7). Stimulation period is indicated by the horizontal line under each trace. Total trace length equals 20 s.

TABLE 3. Response characterizations of single olfactory bulb neurons in Atlantic salmon to water samples of series I. +, excitation; −, inhibition; 0, no effect.

		Sample depth (m)					
Fish No.	Cell No.	0.6	2.8	7.9	10.3	34.3	36.9
1	1	+	+	+	+	+	+
2	2	−	0	0	0	0	0
3	3	+	−	+	+	+	+
3	4	+	+	0	−	0	0
4	5	−	+	+	0	0	0
4	6	0	−	0	0	0	0
4	7	−	+	0	−	−	+
4	8	0	0	0	0	−	0
5	9	0	0	+	0	0	0
6	10	0	0	+	0	0	0
6	11	0	0	0	0	0	0
7	12	−	−	−	−	−	+
8	13	0	0	0	0	0	0

TABLE 4. Response characterization of single olfactory neurons in Atlantic salmon to water samples of Series II. +, excitation; −, inhibition; 0, no effect.

		Sample depth (m)			
Fish No.	Cell No.	1.8	4.7	7.8	25.9
1	1	+	+	+	0
1	2	0	0	−	0
2	3	+	−	−	+
3	4	−	0	0	−
3	5	+	+	+	0
4	6	0	0	+	+
4	7	0	0	0	0
5	8	+	0	0	0
5	9	0	0	0	0
6	10	0	0	0	0
6	11	0	0	0	0
7	12	0	0	0	0
7	13	+	0	+	0
8	14	0	0	0	+
9	15	−	−	−	−
10	16	0	0	0	0

responding neurons, fully 90% could discriminate among the water samples. Of the two different water sample series that were tested, series I was collected near the mouth of the home river and 85% of the neurons tested with that series responded to the samples with 91% of the responding cells able to discriminate among samples. Series II samples were collected 30 km down the fjord from the mouth of the Imsa River and 63% of the cells responded to those water samples. Yet, of those responding, 90% were able to discriminate among the samples collected at different depths.

In a study of bulbar neurons in Arctic char (*Salmo alpinus*), Døving et al. (1974) found that 87% of the neurons were affected by fish tank water. The water samples used in the present study were less efficient stimuli, as only 42% of the bulbar neurons were affected. The response differences of neurons stimulated in the two studies are not necessarily related to the concentration of water and/or odorants derived from the Imsa River. We do not believe that these are "homestream" neurons but are general cells able to recognize differences of

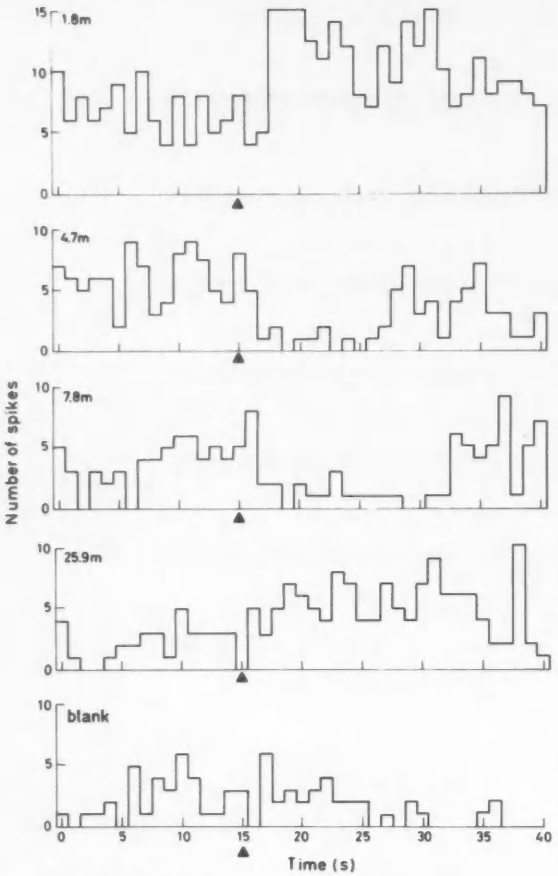

FIG. 9. Summed spike count histograms for olfactory bulb neuron (series II, cell 3) to three successive odor presentations. Stimuli are blank and four water samples taken at the depths in the fjord indicated above each trace.

odor quality in the water samples reflecting the different origins of the layers in the fjord hydrography.

Salmon Orientation

Two major difficulties must be considered in an explanatory model of salmon olfactory orientation in open water, viz. the large-scale horizontal turbulence and the lack of visual points of reference, making rheotactic orientation impossible (Arnold 1974).

Results of our study, combined with those of earlier tracking experiments (Westerberg 1982), allow us to propose the following hypothesis for salmon orientation in the coastal zone. The basic concept is that information for orientation is found locally in the vertical distribution of odorants rather than in a complicated, large-scale horizontal distribution.

All naturally stratified bodies of water have a layered structure. There are almost homogeneous layers containing homestream odorants, which are considered the layers of interest to the salmon. These layers containing specific odorants and their adjacent layers establish a reference system for oriented movement. To maintain its position with respect to the important, information-giving layer, the salmon moves from the layer of interest to the adjacent one with low-amplitude zigzag movements, through the interface layer of strong vertical density gradient. An example of this is shown in Fig. 5.

An interesting similarity to this vertical zigzag motion can be found in the horizontal zigzag pattern of salmon in a stream. Upstream movements of migrating coho salmon have been shown to be rheotactic responses to the artificial homestream chemical signal to which the fish were exposed during smoltification (Johnsen and Hasler 1980). Regions of confluence between two tributaries are characterized by discrete masses of water bearing different scents separated by a common interface boundary between them. Detailed observations of migratory behavior indicate that the fish move along this interface boundary in a zigzag pattern which permits the animal to monitor the edges of the two water masses of different chemical composition (Johnsen 1982). This zigzag behavior in the horizontal plane allows the fish to follow the chemical trail into the correct tributary. In this case the directional cue is the visual contact with the bottom, and it is not possible to make a direct analogue to the vertical zigzag motion.

If the interface of adjacent layers in the ocean becomes indistinct the fish will begin large-amplitude up and down movements to locate another layer of interest. We believe this to be the behavior represented in Fig. 7. Salmon without an olfactory sense will continue to swim up and down with large-amplitude movements in search of a layer of interest. In the absence of odor information the vertical extent of the search is limited only by the physical boundaries; the surface, the bottom, or a strong thermocline. This unsuccessful search behavior is observed for anosmic fish.

The directional cues that are used by the salmon to choose and maintain horizontal swimming direction are unknown. A likely cue is the local direction of the current shear, i.e. the direction of the relative motion of the layer of interest and the adjacent one. Statistically this will be related to the direction to the source of the odorants. If and how this shear can be detected is unclear. One proposal (Westerberg 1984) is that stretching of microscale fluctuations in the gradient layer could be sensed by the fish. If the fluctuations were detected by the olfactory system this should mean a tropotactic orientation. The successful homing of salmon H, which had a unilateral ablation of the olfactory nerve, seems, however, to contradict such a mechanism.

The purpose of our study was not to test the fundamental assumption of the hypothesis — that salmon orient to fine-structure layers. The tracking technique is too imprecise, with occasional hydrographic measurements in the vicinity of the fish, to allow more than some additional support for such an interpretation of the observed behavior. The intent was rather to investigate the role of olfaction within the framework of the hypothesis. Physiologically it is seen that the salmon is able to discriminate the water in adjacent fine-structure layers by olfaction. Behaviorally the loss of the olfactory sense will cause large-amplitude vertical movements that can be interpreted as olfactory search. In future studies it will be important to design experiments to determine which external directional cues are used, such as the current shear, and which sensory systems other than olfaction are required for successful salmon homing.

Acknowledgements

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NOTES

Relative Roles of Food Abundance and Cover in Determining the Habitat Distribution of Stream-Dwelling Cutthroat Trout (*Salmo clarki*)[1]

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Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Can. J. Fish. Aquat. Sci. 42: 1668–1672.

Emigration of wild cutthroat trout (*Salmo clarki*) from laboratory channels over 1-wk trial periods was greater under conditions of low than high food abundance (5 vs. 15% of total trout biomass daily), irrespective of the amount of cover (simulated cover structures added vs. removed). When food abundance was high, emigration of trout was slightly greater under conditions of low than high cover. Cover had no effect on emigration rate when food abundance was low. Trout occurred in association with cover structures when food abundance was high, but not when food abundance was low. These experiments suggest that at summer temperatures, food abundance overrides cover in determining the abundance and microhabitat distribution of adult cutthroat trout within a stream.

L'émigration de la truite fardée (*Salmo clarki*) sauvage de bassins expérimentaux au cours d'expériences d'une semaine était plus élevée dans des conditions de faibles concentrations de nourriture qu'en présence de fortes concentrations (5 vs 15 % de la biomasse totale de truites quotidiennement), indépendamment de la quantité d'abri (couverture simulée ajoutée vs enlevée). Quand la quantité de nourriture était élevée, l'émigration des truites était légèrement plus élevée dans des conditions de faible couverture qu'en présence d'une couverture élevée. Par contre, la couverture n'avait aucune incidence sur le taux d'émigration quand la quantité de nourriture était faible. La truite était présente sous les abris quand la quantité de nourriture était élevée, mais non quand celle-ci était faible. Ces expériences portent à croire qu'aux températures estivales, la quantité de nourriture a plus d'importance que la couverture dans la détermination du nombre de truites fardées adultes présentes dans un cours d'eau et de leur répartition dans les micro-habitats.

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Habitat features, including overhead shading and substrate complexity or associated crevices, have been demonstrated to reduce foraging efficiency of stream fishes, presumably by impairing detection of prey (Ware 1973; Wilzbach and Hall 1985). However, because these features also provide shelter from predation and/or physical disturbances, a trade-off may exist between potential benefits of cover and the cost in reduced foraging gain. Experimental elimination of substrate crevices, for example, increased foraging efficiency of cutthroat trout (*Salmo clarki*) relative to that found for trout in control pools, but probably resulted in an increased mortality (Wilzbach 1984). Dill (1983) reviewed considerable empirical evidence suggesting that fish may be able to adjust habitat use and foraging behavior so as to adaptively balance risks and rewards.

Difficulties in incorporating predation risk into models of foraging behavior or habitat use arise because the units of measurement (i.e. risk of mortality vs. energy or nutritional gain) are not comparable, and Dill (1983) has proposed that one possible solution may lie in observation of fish response to a variety of risk/reward combinations. The choices made by the fish provide a biologically relevant basis for weighting the two factors. In a recent experimental test that followed this approach, Werner et al. (1983) demonstrated that, in the presence of a predator (largemouth bass, *Micropterus salmoides*), small bluegill (*Lepomis macrochirus*) in artificial ponds grew more slowly and restricted their habitat use to areas of low foraging profitability.

Research findings that cutthroat trout are more numerous in cover-poor, logged streams of the Oregon Cascades than in forested streams with abundant cover (Aho 1977; Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983), and that

[1]Riparian Contribution No. 20.

prey availability and foraging efficiency of the trout are likewise greater in logged streams (Wilzbach and Hall 1985), suggest that cover may be less important than prey abundance in determining habitat choice in these systems. The intensity of predation on the trout is not known, but from the documented loss of experimentally confined trout in several pools and the finding of a trout corpse that had evidently been killed by a predator (Wilzbach 1984), and from sightings of avian, reptilian, and mammalian predators at several study sites, at least some risk of predation may be inferred. In this study, to evaluate the relative contribution of food abundance and of cover in determining habitat distribution of cutthroat trout, I examined microhabitat use and emigration of wild cutthroat trout from laboratory channels under varying conditions of food abundance and cover.

Methods

The experiment was conducted in June and July 1984 in recirculating stream channels designed and constructed by Reeves et al. (1983). The channels were oval-shaped, approximately 18 m in total length, and had a water capacity of 5.9 m^3. A 3-m section of each channel that contained a paddle wheel and heating and cooling elements was separated from the experimental area with screening. Escape traps were positioned at these upstream and downstream boundaries. The experimental portion of each channel consisted of an alternating series of riffles and pools, with water velocities ranging from 0 to 10 cm/s. The channel bottom was covered with sand and gravel in the pools, and with small rock (5–8 cm) in the riffles. Water temperature was maintained at 11°C throughout the experiment. The photoperiod was set for a 12-h day.

In trials of 1 wk duration, 10 adult cutthroat trout, ranging in size from 10 to 15 cm, were introduced into a channel. Wild trout were obtained from a resident (nonanadromous) population in Grasshopper Creek (Lane County, Oregon) with a barbless hook and line. The trout were obtained from the same stream in which previous studies of habitat influence on foraging efficiency and growth of the trout were conducted (Wilzbach and Hall 1985; Wilzbach 1984). Experimental fish were measured to the nearest millimetre, weighed to the nearest 0.1 g, and photographed for later identification (Bachman 1984). To acclimate the trout to the water supply and to allow time for recovery from handling stress, they were placed in a holding tank maintained at stream temperature for 48 h prior to introduction to the channel.

Treatment 1 consisted of high food (15% of the total trout biomass daily) and high cover. Fish were fed frozen brine shrimp (*Artemia* spp.) at dawn, noon, and dusk from a food delivery system that simulated natural drift by introducing the food from numerous ports along the entire length of the channel bottom (Reeves et al. 1983). Cover consisted of simulated undercut banks formed by wood shelters and large crevices formed by arrangements of bricks. Cover structures were added only to the upstream half of the channel to provide the trout with a choice in the use of cover. Differences in water velocity between sections of the channel with and without cover structures were insignificant.

Treatment 2 consisted of high food and low cover (no cover structures). Treatment 3 consisted of low food (5% of the total trout biomass daily) and high cover. From pilot experiments, this food level was sufficient to maintain short-term survival but not provide for growth. Treatment 4 consisted of low food and low cover.

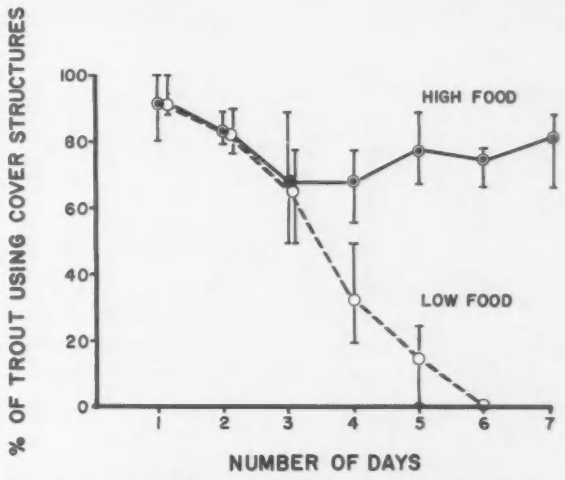

FIG. 1. Percentage of trout present in a channel on a given day that were using cover under conditions of high and low food abundance. Vertical bars represent range of values; $n = 6$ observations.

All treatments were repeated once. To simulate a predation risk and reinforce the use of cover, a battery-powered toy "scuba diver," 200 mm long, was made to swim through each channel at varying times each day. Although not in the legion of predators naturally encountered by the trout, the toy scuba diver effectively frightened the fish throughout the duration of the trial.

Trout use of microhabitat was monitored throughout each trial prior to feeding periods. Trout were observed from the center viewing area of the channels through openings in suspended black plastic curtains that covered the glass channel sides and allowed viewing of the fish without disturbing them (Reeves et al. 1983). Individual trout were identified from photographs by comparison of the lengths and spotting pattern on the body. The tops of the channels were covered with plastic sheets to prevent fish from jumping out. Escape traps were checked three times daily. Emigrants were measured, weighed, and removed from the channels.

Results and Discussion

At high food levels, trout showed strong preferences for cover structures. Little change in this preference occurred between the beginning and end of the trials (Fig. 1). Habitat distribution of the trout did not differ by time of day ($p > 0.10$, Kruskal–Wallis). Fausch (1984) found that trout fry chose cover sites that maximized potential energy gain in a stream aquarium in which predators were absent. In this study, use of cover by trout was likely related only to protection, as differences in water velocity and in prey availability between channel sections with and without cover structures were insignificant.

When food abundance was low, however, use of cover by trout steadily declined (Fig. 1). The percentages of trout that occurred in association with cover differed significantly between high and low food treatments ($p < 0.01$, Kolmogorov–Smirnov). The failure of trout to remain associated with cover structures when food abundance was low is consistent with the finding that, in the cover-rich, forested section of Grasshopper Creek, which has a low abundance of prey (Wilzbach 1984), no relationship existed between numbers of trout inhabiting a pool

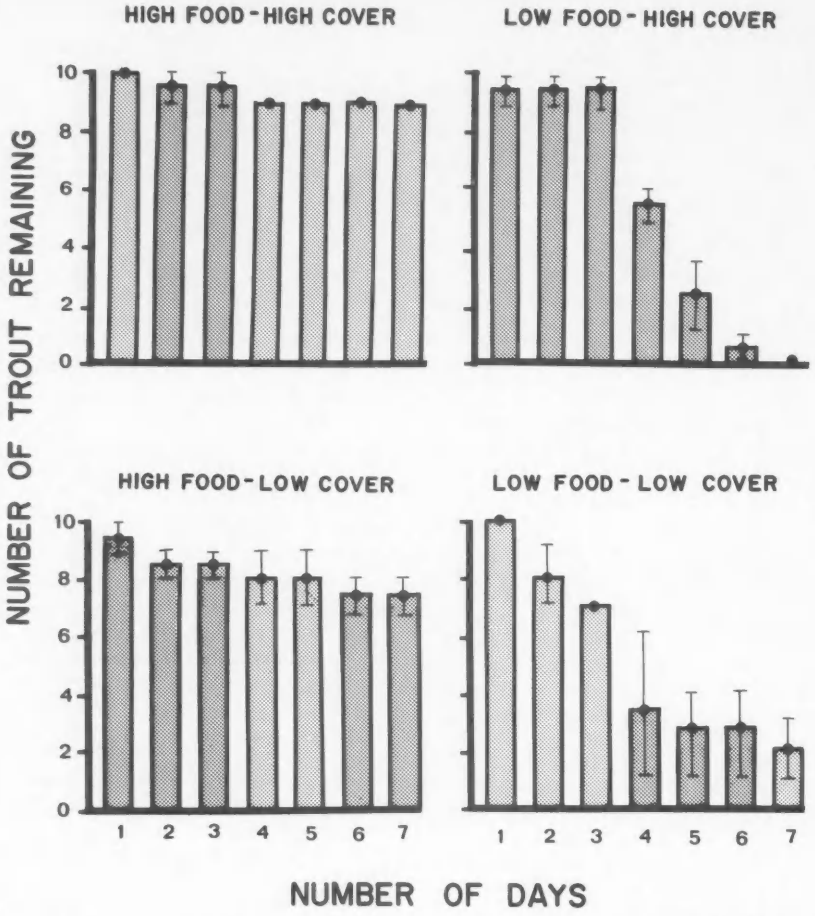

FIG. 2. Mean number of cutthroat trout remaining in channels on each day of a trial under different combinations of food abundance and cover. Vertical bars indicate range of values. All treatments were repeated once.

(1–18 trout per pool in 52 pools) and a qualitative ranking of cover (cumulative sum of a ranking from 0 to 3 of each of seven cover features) ($p > 0.05$, Kendall's rank correlation; unpubl. data).

In treatments lacking cover, cutthroat trout were dispersed throughout the channels, and individual trout changed locations frequently. Differences in the percentage of trout that were positioned in the upstream half of each channel were not significant between high and low food treatments ($p > 0.10$, Kolmogorov–Smirnov).

The numbers of trout remaining in a channel over the 1-wk trial period (Fig. 2) differed significantly between levels of high and low food abundance ($p < 0.01$, Kolmogorov–Smirnov) but not between amount of cover ($p > 0.05$). Classifications by food abundance and cover were associated ($p < 0.01$, 2×2 contingency table). When food abundance was low, however, the number of trout remaining in a channel at the end of a trial was slightly, but significantly, greater under conditions of high than low cover. When food abundance was low, however, the number of trout remaining did not significantly differ between high and low cover. There was little variation between replicates within a treatment. Although decreased emigration of salmonids at high levels of food abundance has been established in previous studies (Symons 1971; Slaney and Northcote 1974; Mason 1976), the influence of a food–cover interaction on emigration has not been reported. Slaney and Northcote (1974) found that, compared with a situation in which trout fry were initially introduced to different food levels, emigration was not as rapid when prey level was reduced from an original level. Data from this study suggest the involvement of a fixed response pattern of trout to changing food availability that consists of use of cover at high food, followed by first movement out of cover, and then emigration at low food.

In all trials, at least one trout emigrated from the channel, suggesting that initial densities exceeded the carrying capacity. Stocking densities (approximately 3.4 trout/m^3 of pool), however, were slightly below densities of trout that were observed in the field (3.7 trout/m^2 in pool in the logged section of Grasshopper Creek). The majority (over 70%) of trout that emigrated from the laboratory channels exited into the downstream traps.

TABLE 1. Weight change ± SD of cutthroat trout that emigrated from channels after 1–6 d and that remained in the channels throughout a 7-d trial. Weight change was measured as final minus initial weight, divided by initial weight, times 100.

No. of days	Weight change ± SD (% body weight)	*n*
1	−2.43±1.18	9
2	−5.50±3.00[a]	2
3	−5.57±2.50	17
4	−5.33±1.51	8
5	−5.20±3.19	5
6	−4.00±2.00[a]	2
7		
Low food	−2.50±2.38	4
High food	+2.94±4.14	33

[a]Range.

Displaced cutthroat trout may in general be more likely to attempt to relocate down rather than upstream because energy costs should be much less.

When provided with a high ration of food, the relative growth rate of trout was greater, but not significantly, in channels with high relative to low cover. However, when provided with a low ration of food, trout tended to lose a relatively greater amount of their body weight in channels with high cover. This may result from a decreased foraging efficiency associated with abundant cover (Wilzbach 1984), or from behavioral deterrents toward feeding in complex habitats (Glass 1971; Savino and Stein 1982). Overall, growth rates of the trout differed significantly between treatments that provided high and low food abundance ($p < 0.01$, Mann–Whitney), indicating that the differences in food rations were biologically meaningful to the trout. The relative growth rate ± SD of cutthroat trout remaining in channels at least 3 d is given below (sample size indicated in parentheses). Relative growth rate (final minus initial weight divided by mean weight, divided by number of days, times 100) is expressed as percent body weight per day:

	High food	Low food
High cover	0.39±0.41 (19)	−1.53±1.06 (19)
Low cover	0.24±0.34 (16)	−1.13±1.15 (14)

Trout emigrated from channels when weight loss approached a fairly narrow band of 2.5–5% of the body weight (Table 1). Trout that emigrated on the first day may have left the channels for reasons unrelated to food abundance (e.g. stress related to changed surroundings), and showed approximately the same weight loss as trout remaining in the channels after 7 d under low food abundance. Trout remaining in the channels after 7 d under conditions of high food abundance gained weight.

Previous studies that reported an increase in salmonid abundance when cover was increased (e.g. Hunt 1976) and a decline in abundance when cover was reduced (e.g. Boussu 1954) evidence the importance of cover (Reiser and Bjornn 1979). Food–cover relationships, however, are complex, and varying requirements of salmonids with species (e.g. Hanson 1977), size of fish (e.g. McCrimmon 1954; Chapman and Bjornn 1969), and season (e.g. Bustard and Narver 1975) may reflect, in part, site-specific differences in disturbance regime, predation intensity, and prey availability. Results of this study corroborate field data suggesting that prey availability is relatively more important than cover in determining distribution and abundance of adult cutthroat trout at summer temperatures in the Oregon Cascades. Assuming that predation poses at least some risk of mortality to trout and that the amount of cover present affects predation risk, one implication is that the habitat response of trout to recent, man-made disturbances may be nonadaptive. Alternatively, trout populations in cover-poor and cover-rich streams may simply adopt different strategies for dealing with environmental uncertainty. Longer term studies, encompassing estimates of reproduction through several year classes, are necessary to determine which alternative may apply.

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Quadratic Discriminant Analysis with Covariance for Stock Delineation and Population Differentiation: A Study of Beaked Redfishes (*Sebastes mentella* and *S. fasciatus*)

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Misra, R. K. 1985. Quadratic discriminant analysis with covariance for stock delineation and population differentiation: a study of beaked redfishes (*Sebastes mentella* and *S. fasciatus*). Can. J. Fish. Aquat. Sci. 42: 1672–1676.

Stock delineation is of vital importance in fisheries management programs. Linear discriminant function (LDF) has been employed extensively in population differentiation studies but is of severely restricted usefulness when populations differ in their dispersion matrices. Quadratic discriminant function (QDF) is the appropriate analysis to employ in these situations. Here, I analyzed morphometric data of beaked redfishes (*Sebastes mentella* and *S. fasciatus*) by a recently developed conditional QDF.

L'identification des stocks revêt une importance vitale pour les programmes de gestion halieutique. Les études d'identification de populations font souvent appel à une fonction discriminante linéaire, mais l'utilité de cette dernière est grandement restreinte quand les matrices de dispersion des populations varient. Dans ces cas, l'analyse appropriée à utiliser est une fonction discriminante quadratique. L'auteur analyse des données morphométriques sur le sébaste (*Sebastes mentella* et *S. fasciatus*) à l'aide d'une fonction discriminante quadratique conditionnelle récemment mise au point.

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Stock delineation is of vital importance in fisheries management programs. Effective management of a species depends on the reliability of our knowledge of distribution and biological characteristics of individual stocks. The distinction between deepwater redfish (*Sebastes mentella*) and Labrador redfish (*S. fasciatus*), although vital for the effective management of redfish resources in the Northwest Atlantic, has been less than clear for decades (Misra and Ni 1983; Ni 1981a, 1981b). Macdonald and Pitcher (1979) developed a method of analyzing distribution mixtures, at the univariate level, and applied it to estimate age-group parameters from size–frequency data. Morphometric measurements have frequently been used to differentiate populations in general (see e.g. Blackith and Reyment 1971; Ihssen et al. 1981; Misra and Ni 1983) and stocks of fish in particular (see e.g. Almeida 1982; Casselman et al. 1981; Davidson et al. 1982; Ihssen et al. 1981; Sharp et al. 1978). In a stock discrimination analysis of capelin in the Gulf of St. Lawrence, Sharp et al. (1978) noted that morphometrics offered greater potential in separating capelin (*Mallotus villosus*) stocks than meristics.

Fisher's discriminant function has been employed extensively, by the most conservative standards, in behavioral, biological, business, fisheries, medical, and social research (Goldstein and Dillon 1978). "Even when two similar species can be identified with a single measurement, a combined criterion of two or more may increase the separation between them" (Bliss 1970). The

TABLE 1. Means and ranges (mm) of eight morphometric characters Y_i, $i = 1, \ldots, 8$, for *S. mentella* ($n = 99$) and *S. fasciatus* ($n = 99$). All measurements were transformed to common logarithms.

		S. mentella		*S. fasciatus*	
Y_i	Character description	Mean	Range	Mean	Range
1	Head length	2.0021	1.8325–2.1772	1.8211	1.7634–1.9685
2	Preanal length	2.2471	2.0846–2.4190	2.0991	2.0158–2.2480
3	Pectoral fin base	1.3462	1.1790–1.5198	1.2184	1.1335–1.3856
4	Anal fin base	1.6122	1.4330–1.7528	1.4438	1.3522–1.6107
5	Length of longest pelvic ray	1.6730	1.4914–1.8156	1.5486	1.4265–1.6776
6	Length of longest pectoral ray	1.8386	1.6484–1.9845	1.6712	1.6085–1.8312
7	Dorsal length of caudal peduncle	1.5957	1.3324–1.7679	1.4351	1.3263–1.5888
8	Standard length	2.4243	2.2742–2.5763	2.2725	2.2041–2.4133

following are noted:

(1) Discriminant functions are employed when the existence of reference samples can be assumed on the basis of an external criterion (Kendall and Stuart 1976).

(2) Discriminant analysis of morphometric data done in the past has generally been unsatisfactory due to sampling bias associated with the varying size of individuals and the large overlapping of measurements. These difficulties are almost invariably encountered in a stock delineation study. To overcome these, Misra and Ni (1983) employed linear discriminant function (LDF) with covariance to discriminate between *S. mentella* and *S. fasciatus*. Individuals vary within populations, as in standard length, to warrant correction as in a discriminant function which is adjusted by covariance (Bliss 1970).

(3) Morphometric measurements are particularly appropriate in a discriminant analysis, as these are taken on "continuous" variables and multivariate normality is closely approximated by their logarithms (Bliss 1967; Misra and Ni 1983; Pimentel 1979). Performance of LDF in non-normal situations is very misleading (Dillon 1979; Lachenbruch et al. 1973).

LDF is valid when the two populations are multivariate normal with different mean vectors of variates, but identical dispersion (or variance–covariance) matrices (Kendall and Stuart 1976). When two populations have unequal dispersions, discriminant score for each population will have quadratic terms in the variates. LDF then is of severely restricted usefulness and must, indeed, be replaced by quadratic discriminant functions (QDF) (Kendall and Stuart 1976).

Rawlings et al. (1985) examined the two-group discriminant analysis problem where each observation vector, consisting of the discriminators and covariates, comes from one of the two multivariate normal populations with unequal dispersion matrices. As inequality of group dispersions may be of a common occurrence as in the redfish data of Misra and Ni (1983), the method of Rawlings et al. (1985) will be very useful in population differentiation studies. My objectives were (1) to present the method of Rawlings et al. (1985) briefly, after reorganizing it following Li (1964) and Rao (1973), and (2) to reanalyze the redfish data of Misra and Ni (1983) by this new method.

Materials and Methods

As this information is provided in detail in Misra and Ni (1983) and Ni (1981a, 1981b), it is given here only briefly. Prior to doing the LDF analysis of Misra and Ni (1983), specimens of *S. mentella* and *S. fasciatus* were separated into two groups on the basis of the extrinsic gas bladder musculature. Identification by extrinsic gas bladder musculature requires the tedious and technical work of dissecting a fish. Use of extrinsic gas bladder musculature as a direct measure of misclassification is, therefore, not feasible where several (hundreds) fish need to be identified. Twelve morphometric characters (listed in table 1 of Misra and Ni 1983) were measured on an individual specimen. All measurements were transformed to (common) logarithms for reasons explained earlier in the text. Misra and Ni (1983) noted that parsimony in the number of variates to be included in a discriminant analysis is desirable when sample sizes are small. This is, however, not necessary when analyzing large samples (as in this study) although omitting variables with nonsignificant discriminant coefficients will increase the stability of the discriminant function (Bliss 1970). Misra and Ni (1983) demonstrated that for their redfish data only seven discriminators were effective. Their LDF was therefore based on eight characters, i.e. the seven discriminators and the covariate, standard length. Those characters are listed in Table 1.

For their LDF, Misra and Ni (1983) employed only "complete" specimens, i.e. specimens for which all eight measurements were available because "missing observations virtually destroy morphometrics" (Pimentel 1979). Each sample had 99 complete specimens. Table 1 gives means and ranges of these characters Y_i, $i = 1, \ldots, 8$. Based on eight characters, there were 99 complete specimens in *S. mentella*, as opposed to 97 in table 1 of Misra and Ni (1983) which were identified on the basis of 12 characters. Consequently, some of the mean values shown in Table 1 here do not match with those shown in table 1 of Misra and Ni (1983).

Let (1) n_i, $i = 1, 2$, be the size of the sample drawn from population P_i and (2) $\boldsymbol{Y}_i$ be the $p \times 1$ vector of observations on individual k, $k = 1, \ldots, n_i$, from P_i. For the redfish study of Misra and Ni (1983), $p = 8$. For the p-variate normal distribution of the observation vector from P_i, let the mean vector be denoted as $\boldsymbol{\mu}_i$ and the dispersion matrix as $\boldsymbol{A}_i$. The discriminant score for the ith population is

$$S_i = -\tfrac{1}{2} \ln |\boldsymbol{A}_i| - \tfrac{1}{2}(\boldsymbol{Y} - \boldsymbol{\mu}_i)' \boldsymbol{A}_i^{-1} (\boldsymbol{Y} - \boldsymbol{\mu}_i) + \ln \pi_i$$

where π_i is the prior probability for the ith population. In a discriminant analysis when the prior probabilities are not known and population parameters $\boldsymbol{\mu}_i$ and $\boldsymbol{A}_i$ are substituted by their sample values, the prior probabilities are taken to be proportional to observed numbers of the two species in the sample that was classified on the basis of extrinsic gas bladder musculature (Rao 1973). The conditional QDF of Rawlings et al. (1985) leads to a classification rule that is used to discriminate between two populations by computing the difference $S_1 - S_2$, after adjusting for differences in the covariate.

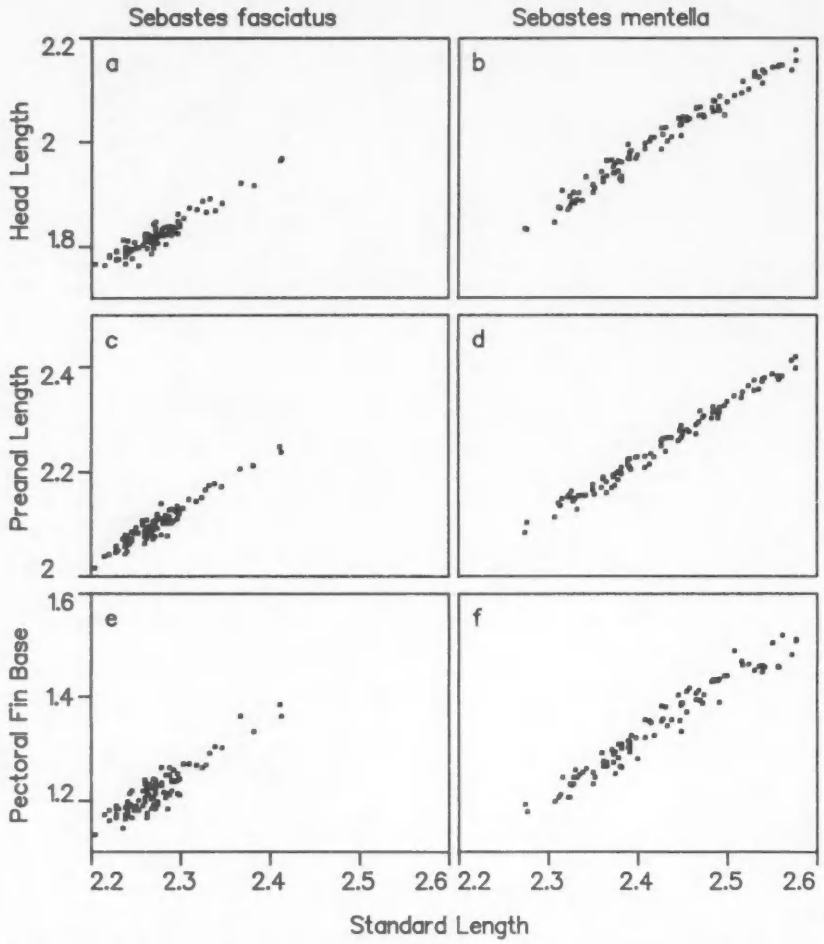

FIG. 1. Bivariate scatter plots of the covariate and the variates to compare dispersions for *S. fasciatus* and *S. mentella*. All measurements were transformed to common logarithms of millimetres.

Li (1964) stated that (1) adjustment may be done at any meaningful value of the covariate, Y_8 (Table 1), and (2) the value most frequently chosen would be the overall mean of Y_8. For convenience of expressing the conditional QDF in a pleasant form, random vector of discriminators Y_i, $i = 1, \ldots, 7$, is denoted as $\boldsymbol{X}$ and the covariate Y_8 as $\boldsymbol{Z}$. Also, mean vector $\boldsymbol{\mu}_i$ is expressed as $(\boldsymbol{\mu}'_{x_i}, \mu_{z_i})'$ and the dispersion matrix $\boldsymbol{A}_i$ as

$$\begin{bmatrix} A_{xx_i} & A_{xz_i} \\ A_{zx_i} & A_{zz_i} \end{bmatrix}.$$

The conditional QDF is then given as follows:

$$\text{QDF} = \tfrac{1}{2} \ln (|\boldsymbol{B}_2|/|\boldsymbol{B}_1|) - \tfrac{1}{2}(\boldsymbol{X} - \boldsymbol{\alpha}_1)'\boldsymbol{B}_1^{-1}(\boldsymbol{X} - \boldsymbol{\alpha}_1) + \tfrac{1}{2}(\boldsymbol{X} - \boldsymbol{\alpha}_2)'\boldsymbol{B}_2^{-1}(\boldsymbol{X} - \boldsymbol{\alpha}_2)$$

where $\boldsymbol{B}_i = A_{xx_i} - A_{xz_i} \cdot A_{zz_i}^{-1} \cdot A_{zx_i}$ and $\boldsymbol{\alpha}_i = \boldsymbol{\mu}_{x_i} - A_{xz_i} \cdot A_{zz_i}^{-1}$ $(z - \mu_{z_i})$ for $i = 1, 2$ are conditional dispersion matrices and covariance adjusted vector of means, respectively. An individual is assigned to that population for which the QDF score is larger, i.e. assign an individual to P_1 when conditional QDF $>$ $\ln (\pi_2|\pi_1)$ and to P_2 otherwise.

Rawlings et al. (1985) employed the leave-one-out estimator (also see Kshirsagar 1972) for the actual error rate for the sample based conditional QDF. First, observations are removed, one at a time. Then the conditional QDF is estimated based on the remaining observations. This is followed by a record of whether it is misclassified. The estimated expected actual error rate is calculated as

$$\sum_{i=1}^{2} (\pi_i f_i / n_i)$$

where f_i is the number of misclassified observations for the ith sample.

Analysis and Results

Specimens of *S. fasciatus* were generally smaller than those of *S. mentella* and the range of morphometric characters overlapped broadly between groups (Table 1). In their analysis of the redfish data, Misra and Ni (1983) employed the LDF where

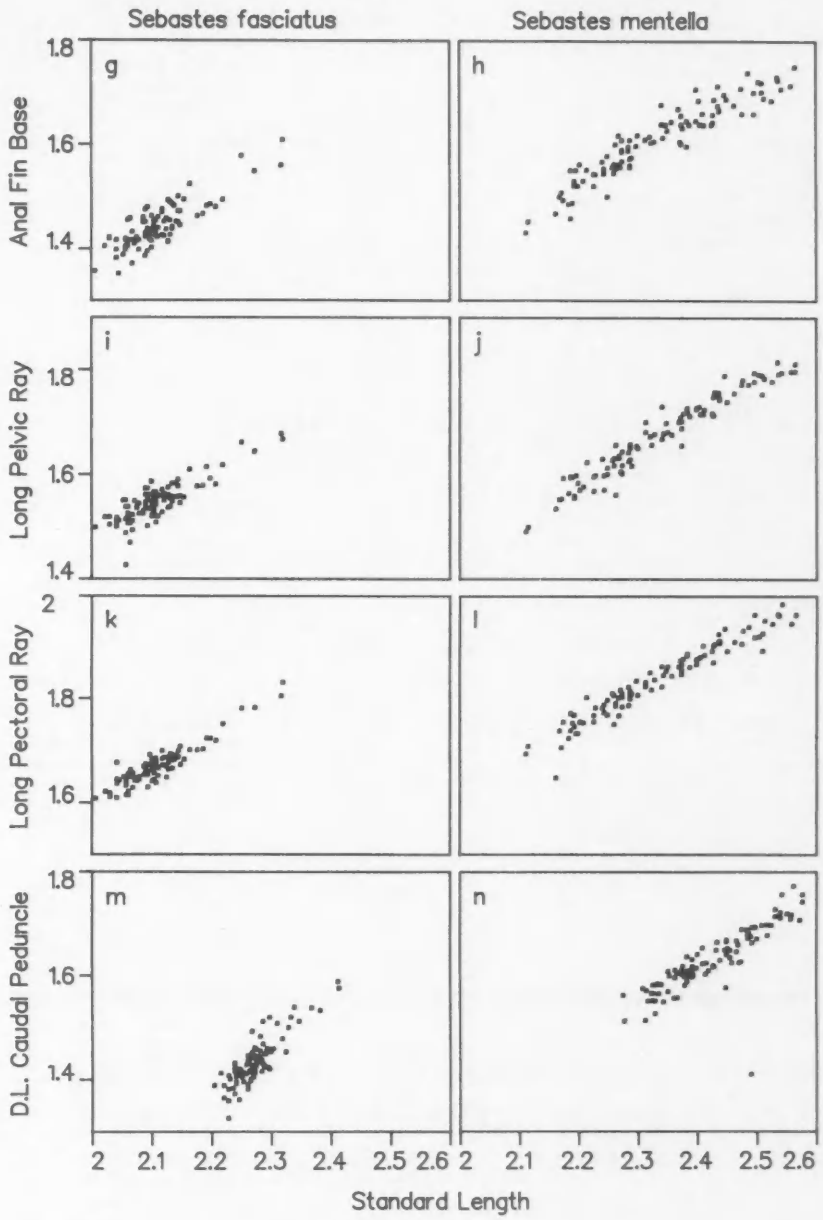

FIG. 1. (*Concluded*)

vectors of means of discriminators were adjusted for inequalities in standard length. They also noted that large overlaps of ranges (46% in *S. mentella* and 67% in *S. fasciatus*) of Y_8 or Z and its inadequacy to discriminate between the two species effectively provided additional support for using standard length as a covariate.

Figure 1 shows the bivariate scatter plots of the covariate (abscissa) and each of the variates (ordinate) Y_i, $i = 1, \ldots 7$, for *S. fasciatus* and *S. mentella*. It is recalled that the two samples here had exactly the same number (viz. 99) of observations. To further facilitate visual comparison of the two dispersions, I employed same scales of measurement for the two samples in each plot.

Unequal group dispersions are obvious in the figure; the ellipse (of scatter of points) for *S. mentella* is elongated and thinner whereas that for *S. fasciatus* is shorter and wider. These observations were confirmed, statistically, as follows: null hypothesis of equality of the conditional dispersion matrices B_i, $i = 1, 2$, of discriminators was tested by the modified generalized likelihood-ratio statistic explained (e.g. in Morrison 1976). This null hypothesis was rejected ($p \leq 0.0001$), thus indicating the following: (1) The assumption of the equality of dispersion

matrices underlying the use of the LDF with covariance by Misra and Ni (1983) was not justified. (2) Conditional QDF, and not the LDF with covariance that Misra and Ni (1983) employed, would provide the appropriate discriminant analysis for the redfish data. Analysis of the redfish data by the conditional QDF was therefore done following the procedure explained earlier in the text. This analysis was followed by an estimate of the actual error rate for the sample based conditional QDF. The leave-one-out estimator identified a total of 24 misclassified individuals, which included 20 *S. mentella* and 4 *S. fasciatus*, from 198 specimens. The estimated expected error rate was thus 12% thus indicating that classification by the conditional QDF had been quite useful.

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Short-term Effect on the Metabolism of Lotic Benthic Communities Following Experimental Acidification

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Short-term quantitative change in whole benthic community metabolism was observed at low pH. From the beginning until 38 d after acidification (with one exception), oxygen uptake was significantly lower in the acidified channels (pH 4.0, pH 4.0 + 0.4 mg Al·L^{-1}) than in the control (pH 6.3–6.9, 0.05–0.13 mg Al·L^{-1}). By the midpoint of acidification (45 d) until the end (85 d), oxygen uptake of the communities in treated channels did not differ from the control. However, at the end of the experiment in acidified channels, the biomass of macroinvertebrates and algae were higher and the number of macroinvertebrates was lower than in the control. The lower total community metabolism may result in a lower decomposition rate, as organic matter in sediment was higher in acidified channels with or without aluminum (58 and 54%, respectively) than in the control (46%).

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Des modifications quantitatives de courte durée du métabolisme de communautés benthiques soumises à une acidification expérimentale ont été observées. Du début de l'acidification jusqu'au 38ième jour (sauf à une exception), il y a une réduction significative de la consommation d'oxygène dans les canaux acidifiés (pH 4,0 et pH 4,0 + 0,4 mg Al·L^{-1}) comparativement au canal témoin (pH 6,3–6,9, 0,05–0,13 mg Al·L^{-1}). A partir du 45ième jour jusqu'à la fin de l'expérience (85ième jour), il n'y a plus aucune différence dans le métabolisme des communautés soumises ou non à l'acidification. Par contre, à la fin de l'expérience, les biomasses du périphyton et des invertébrés sont plus importantes en milieu acidifié, alors que le nombre d'invertébrés y est plus faible. La réduction du métabolisme en milieu acidifié semble influencer les processus de décomposition. En effet le pourcentage de matière organique trouvé dans les sédiments acidifiés, avec ou sans aluminium (58 et 54 % respectivement) est plus élevé que dans le témoin (46 %).

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The effects of acidification on aquatic benthic communities were studied by several authors and are reviewed in Haines (1981) and D'Itri (1982). Few of these studies were concerned with the influence of acidification upon the metabolism of benthic communities.

In lakes, Gahnstrom et al. (1980) could not detect any difference in the glucose turnover time or in oxygen uptake by sediments collected from five acidified and two nonacidified oligotrophic lakes. Anderson et al. (1978), however, found reduced sediment oxygen consumption and carbon dioxide production, and an increased glucose turnover rate in microcosms in lakes where pH was around 5.0 compared with lakes around pH 6.0. Haines (1981) suggested that such contradictory findings may result from the use of different techniques of sediment manipulations. Differences in oxygen uptake by the sediments could also be explained by the trophic status of the lakes. Differences in the taxonomic composition of benthic communities, in the state of acidification, and in concentrations of heavy metals may also modify response.

Results obtained in lakes may not apply to streams. The study by Traaen (1980) is the only stream study that has measured metabolism. That experiment showed that oxygen consumption of leaf litter substrate, without macroinvertebrates, was reduced by 50% when the pH was lowered from 7.0 to 5.2.

In this study, our objective was to compare the role of selected experimental conditions (acidification at pH 4.0 with or without aluminum) on the metabolism of the total benthic community in seminatural conditions, with reference to a control of pH 6.3–6.9.

Methods

The study site, the experimental setup, and acidification procedures were given in detail in Sérodes et al. (1984) and are summarized as follows. Experiments were conducted in June–October 1983 in three parallel channels fed by a small creek. After a colonization period of 41 d, treatments were initiated. One channel (A) was acidified to pH 4.0 with H_2SO_4. Another (channel AA) was acidified at the same pH and enough aluminum sulfate was added to increase the aluminum to 0.37 ± 0.06 mg Al·L^{-1}. The third channel (C) was fed with unaltered creek water (pH 6.3–6.9, 0.05–0.13 mg Al·L^{-1}).

Variations in substrate and flow conditions were eliminated in our system; thus, before acidification, temporal evolution of the benthic fauna was similar between channels (Sérodes et al. 1984). The metabolism determination made prior to acidification (day −1) confirmed that all channels were similar. After acidification, metabolism was measured on days 7, 14, 27, 38, 45, 58, 72, and 85. On each occasion, measurements were obtained in three respirometry chambers (Fig. 1) per channel. Oxygen concentrations were determined by the micro-Winkler technique (Fox and Wingfield 1938), immediately after closing the cover of the chamber, and after 2 and 4 h of incubation. Water subsamples (20 mL) were withdrawn from each chamber

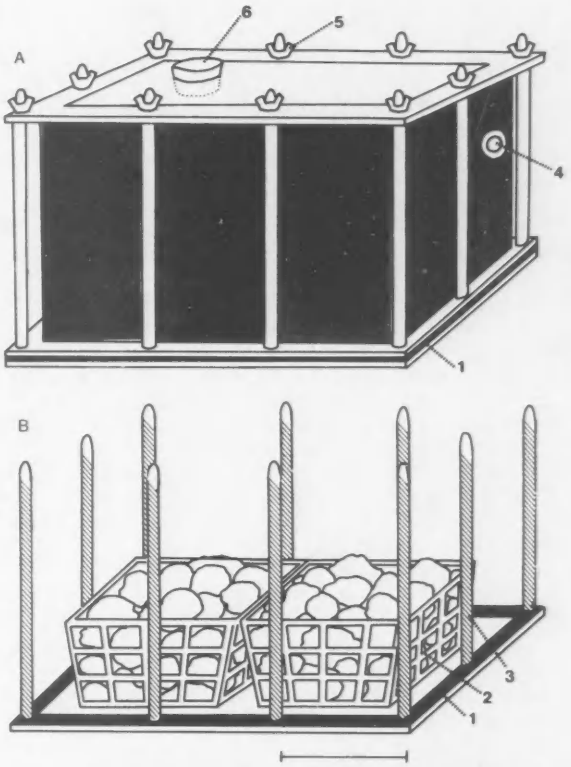

FIG. 1. Respirometry chamber. (A) Respirometry chamber assembled; (B) permanent base unit. Before measurements, the rubber gasket (1) was cleaned and the Plexiglas cover with black sides was tightly joined to the base unit with stainless bolts (3) and wingnuts (5). Special care was taken to avoid the formation of bubbles on the inner sides of the box. After inserting the rubber stopper (6), the top of the box was also darkened. Water samples for oxygen determination were withdrawn through a vacutainer stopper (4). Plastic baskets (2) (10 × 10 × 8 cm) full of granitic pebbles (2.5–4.0 cm) were used as artificial substrates. Bar scale = 10 cm.

through a vacutainer stopper (Fig. 1) with a gas-tight syringe. Oxygen saturation values at the beginning of the measurements were 78–86% and were usually 69–80% at the end. Exceptionally, two values of 56% were recorded when the water temperatures were high (16–18°C). At the end of the incubation period, the chamber was opened and the baskets holding the communities and the permanent base unit of the chamber were left in place for subsequent measurements. The same communities were followed through time. Finally, after the last metabolism measurement (day 85), organisms and sediments from each chamber were collected, number and biomass (dry weight) of benthic invertebrates were estimated, and dry weight (100°C for 24–48 h) and ash-free dry weight (500°C for 1 h) of the sediment were determined. Biomass of periphytic algae was also assessed; unglazed ceramic tiles located on top of baskets were scraped and chlorophyll *a* was extracted in absolute methanol (Marker et al. 1980); correction was made for phaeopigments.

The use of this type of respirometry chamber, which eliminates flow, could lead to underestimation of the metabolism (Odum 1957). Various systems have been proposed to insure circulation of water inside the chamber (Osborne and Davies 1981; Grimm and Fisher 1984). None of these systems assures creation of flow conditions identical to natural ones, or eliminates accumulation of metabolites in the water of closed chambers. Since our objective was to compare the metabolism of communities submitted to two experimental conditions, we chose the simplest system, in which bias was constant, and in which conditions were similar from one chamber to another.

The choice of this type of chamber was also governed by our intention to follow the same communities through time, without disturbing them at each measurement; moreover, the nine cycles of measurements did not induce nine cycles of drift and recolonization in the baskets from respirometry chambers, since after termination of experiment (day 85), abundances of macroinvertebrates were similar or higher in baskets from the chambers than in baskets from the channel.

Kruskal–Wallis nonparametric tests were used to compare data between channels.

Results

In all sets of measurements, either prior to or following acidification, initial oxygen concentrations (0 h) were not statistically different among the three channels; saturation values in the chambers were between 78 and 86% and similar to values found in the channels.

Prior to acidification (day −1), community metabolism in the three channels did not differ significantly ($p > 0.1$). Mean uptake rates in each channel were 0.51, 0.49, and 0.54 mg $O_2 \cdot L^{-1} \cdot h^{-1}$ (Table 1).

On day 7, after acidification, the oxygen uptakes, with or without aluminum, were respectively 0.18 and 0.20 mg $O_2 \cdot L^{-1} \cdot h^{-1}$ and 0.31 and 0.28 mg $O_2 \cdot L^{-1} \cdot h^{-1}$ on day 11. For the same period, uptake rates were 0.58 and 0.59 mg $O_2 \cdot L^{-1} \cdot h^{-1}$ in the control channel. These results show an important and significant decrease ($p < 0.05$) in oxygen uptake in acidified chambers relative to controls.

From day 14 to 85, differences between acidified and control channels became progressively attenuated. After day 27, uptake rates did not differ significantly between control and acidified chambers (except on day 38). During this period, oxygen uptake rates in control went from 0.59 to 0.07 mg $O_2 \cdot L^{-1} \cdot h^{-1}$ as water temperature lowered from 18 to 4°C.

TABLE 1. Uptake rates in respirometry chambers before (day −1) and on days 7, 14, 27, 38, 45, 58, 72, and 85 after acidification, $\bar{X} \pm$ SE of three replicate chambers per treatment: C, control; A, acid; AA, acid + Al. *Statistical difference ($p < 0.05$).

Day	T (°C)	Uptake rates (mg $O_2 \cdot L^{-1} \cdot h^{-1}$) C	A	AA
		Before acidification		
−1	18	0.51±0.03	0.49±0.06	0.54±0.02
		After acidification		
7	15	0.58±0.02	0.20±0.07	0.18±0.04*
14	18	0.59±0.04	0.28±0.02	0.31±0.06*
27	15	0.46±0.08	0.31±0.02	0.28±0.07
38	13	0.38±0.04	0.22±0.04	0.22±0.07*
45	16	0.40±0.05	0.30±0.07	0.35±0.01
58	11	0.26±0.03	0.24±0.04	0.23±0.02
72	12	0.12±0.04	0.15±0.05	0.22±0.03
85	4	0.07±0.02	0.16±0.05	0.10±0.01

At the end of experimentation (85 d of treatment), the biomass of invertebrates was significantly greater ($p < 0.01$) in the acidified chambers than in the controls (Table 2), while total numbers of benthic invertebrates per basket in acidified chambers were significantly lower ($p < 0.01$) than in the control chambers (Table 2). Difference between acidified and nonacidified channels followed the same pattern (C: 682 ± 23.2, AA: 299 ± 14.2, A: 386 ± 27.8). Values for the control, however, were two times lower in baskets from the channel than in baskets from chambers; taxonomic composition in baskets from the channel and in the chambers was similar.

On day 85, no significant difference in mean dry weight of the sediments between the experimental conditions was apparent. However, percent of organic matter was significantly greater ($p < 0.01$) in acidified than in control chambers (Table 2).

At the same period, values of chlorophyll *a* in the three channels differed significantly ($p < 0.01$). Chlorophyll *a* in the control was low (2.5 mg $\cdot m^{-2}$); it was 3.5–5 times higher in the acidified channels (Table 2). Filamentous algae thickly covered the sides of acidified channels but were inconspicuous in the control channel.

Discussion

Our system was designed to enable us to make metabolism comparisons between channels and consequently between pH or aluminum levels. As oxygen uptake rates were not statistically different among channels before acidification, we felt confident that any deviation from the control in acidified channels would be a good indication of stress brought about by the addition of strong acid (H_2SO_4) with or without aluminum.

This stress observed in the first half of the acidification period may be attributed to a lower uptake by microorganisms. Organic matter was high in sediment (46% in the control), and the microorganism community is important for decomposition processes (Kaushik and Hynes 1971). Lower metabolism may result in a lower decomposition rate, thus in an accumulation of organic matter, although this accumulation may also result from mechanical causes. Complexation of organic matter with aluminum might be possible. And flocculation of resulting complexes may have increased the organic matter in the sediment.

Accumulation of organic matter in acidified lakes was pre-

TABLE 2. Macroinvertebrates and sediments in respirometry chambers after 85 d of treatment, and chlorophyll *a* values in the three channels at the same time. Data represent mean ± SE (*n*). C, control; A, acid; AA, acid + Al. $^{**}p < 0.01$ between treatments.

	Macroinvertebrates		Sediments		
	Total no. per basket**	Dry weight per basket (g)**	Dry weight per basket (g)	Organic matter (%)**	Algae chlorophyll *a* ($mg \cdot m^{-2}$)**
AA	383.7±30.7 (3)	0.0617±0.0091 (3)	1.21±0.2 (2)	58.6±1.7 (2)	8.8±3.0 (4)
A	417.7±14.2 (3)	0.0555±0.0036 (3)	1.18±0.1 (3)	54.1±0.1 (3)	12.2±3.3 (4)
C	1157.7±51.9 (3)	0.0347±0.0051 (3)	1.17±0.1 (3)	46.4±1.0 (3)	2.5±0.8 (4)

viously reported by Grahn et al. (1974). It may be attributed to lower bacterial counts in acidified water. But, results from counts are rather contradictory: no difference was observed by Scheider et al. (1979) and Muller (1980), while Rao and Dutka (1983) found that bacteria submitted to an acid stress can be decimated.

Other studies in streams suggested that decomposition was slower in acid water (Minshall and Minshall 1978; Traaen 1980). There is some degree of confusion, however, as Arnold et al. (1981) could not find such differences. Traaen (1980) also showed that oxygen consumption of leaf litter packs was reduced in acidified water. A reduced attack by the benthos may also slow down decomposition processes. In our system, the benthic biomass was higher in the treatments than in the reference channel; the fauna was dominated by chironomids (M. Allard and G. Moreau, unpubl. data) that feed heavily on detritus. Therefore, a reduction in decomposition processes in acidified conditions cannot be attributed to a lower biomass of macrobenthic detritivores but only to a less efficient microorganism community.

In the last half of the acidification period, similar oxygen uptake rates among conditions could be explained by (1) modifications in the various components of the community or (2) a recovery of microorganism communities. Both explanations may be realistic. The benthic community of acidified channels is clearly modified compared with the reference: lower total numbers of macroinvertebrates but higher biomass in acidified channels, while chlorophyll *a* values of periphytic algae were 3.5–5 times higher in acidified channels. Rates of uptake in control chambers were lower towards the end of experiment as a result of lower temperature. As for the second explanation of recovery in microorganism communities, results obtained by Boylen et al. (1983) showed that some bacteria present in neutral water could also tolerate low pH, and may become important as time progresses.

Results from acidified channels with or without aluminum are similar, and indicate that pH drop is the important factor generating effects on the benthic community metabolism.

Effects of a sudden short-term acid stress during snowmelt or during heavy rainstorms could be more important than long-term acidification, especially if long-term adjustment to acid conditions can take place. Even though the metabolism of the community seems to recover progressively under acidic conditions (with or without aluminum), decomposition processes overall may not recover, since organic matter accumulates in acidified channels. A lower decomposition, particularly in streams, where allochthonous matter represents the major contribution of energy input in the system, could be a serious threat to an acidified ecosystem.

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PERSPECTIVES

The Niagara Labyrinth — The Human Ecology of Producing Organochlorine Chemicals[1,2]

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Gilbertson, M. 1985. The Niagara labyrinth — The human ecology of producing organochlorine chemicals. Can. J. Fish. Aquat. Sci. 42: 1681–1692.

Organochlorine chemical production, by United States chemical manufacturers, has resulted in severe contamination of the Niagara River, Lake Ontario, and the St. Lawrence River and of Canadian resources by transboundary pollution. In 1978, Canada and the United States signed the second Great Lakes Water Quality Agreement which was designed to overcome toxic chemical as well as eutrophication problems. This paper is a review of the effectiveness of the implementation of the provisions of the 1978 Agreement concerning toxic chemicals. To aid with organization of the material the sociological framework of human ecology has been employed. To focus the discussion on the more important facets, the critical pathway analysis methodology, developed for radiation protection, has been used.

La production de produits chimiques organochlorés, par des fabricants américains, a entraîné une contamination sérieuse de la rivière Niagara, du lac Ontario et du fleuve Saint-Laurent ainsi que de ressources canadiennes par le biais de la pollution transfrontalière. En 1978, le Canada et les États-Unis ont signé la deuxième entente sur la qualité de l'eau des Grands Lacs, laquelle visait à surmonter les problèmes liés aux substances toxiques et à l'eutrophisation. Dans cet article, on examine l'efficacité de la mise en œuvre des dispositions de l'entente de 1978 concernant les produits toxiques. On a adopté le cadre sociologique de l'écologie humaine pour faciliter l'agencement de la documentation. On s'est servi de la méthode de l'analyse des voies critiques, élaborée en vue de la protection contre les radiations, pour faire porter la discussion sur les aspects les plus importants.

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The Great Lakes are an enormous freshwater resource in the heart of the North American continent and store about one fifth of the world's freshwater supplies. The international boundary between the United States and Canada runs through four of the five Great Lakes and administration is therefore divided between two countries, one province, and eight states. With the growth of population and industry, water quality and water quantity have remained continuing issues in bilateral relations. In 1909, Britain and the United States successfully concluded negotiations for a Boundary Waters Treaty with provisions for setting up an International Joint Commission to examine, report on, and adjudicate matters of difference referred to it. In 1964, Canada and the United States referred the matter of pollution of the lower Great Lakes (Lake Ontario and Lake Erie) to the International Joint Commission to investigate and report on the extent of pollution. The successful completion of the reference led to the signing of the 1972 Great Lakes Water Quality Agreement which was mainly concerned with control of phosphates to reverse the process of eutrophication. In 1978, a revised Great Lakes Water Quality Agreement was signed with a greater emphasis on control of toxic chemicals which had come to be perceived as an increasing threat.

The William H. Donner Foundation, with head offices in New York, has as one of its goals the promotion of United States understanding of Canada through study of United States relationships with Canada. In 1983, the Donner Foundation, in consultation with the staff of the International Joint Commission, requested the U.S. National Research Council to study the Great Lakes Water Quality Agreement. Following a bilateral conference in 1984 (National Research Council 1984) the Donner Foundation sponsored a Committee of the Royal Society of Canada and the U.S. National Research Council to evaluate the effectiveness of the 1978 Agreement. This paper was prepared at the request of the Canadian Chairman, Dr.

[1]Review of the 1978 Great Lake Water Quality Agreement, sponsored by the William H. Donner Foundation. Presented to the Committee of the Royal Society of Canada and National Research Council, Ottawa, Ont., February 13, 1985.

[2]The views expressed in this paper are those of the author and do not necessarily reflect the views of the Department of Fisheries and Oceans or of the Government of Canada.

Henry Regier, as a personal perspective of the effectiveness of the Agreement for presentation to the Committee.

The idea of using an independent source of funding, such as the Donner Foundation, to sponsor a study of the effectiveness of the 1978 Great Lakes Water Quality Agreement is an innovative step toward improving bilateral harmony. Both Articles VII and X of the Agreement acknowledge the need for comprehensive review of the operation and effectiveness of the programs and other measures established pursuant to the Agreement. My reading of the 1978 Agreement is that it was an admission by Canada and the United States that, although they had solved many of the problems caused by eutrophication, there was still an enormous problem of toxic chemicals that remained largely unaddressed by the previous 1972 Agreement. It is now 7 yr since the 1978 Agreement was signed. How can we judge whether it has been effective? Do we look at the monitoring data on fish and gulls and say that because the levels of certain contaminants are lower than 10 yr ago we have been effective? Or should we look at the evidence of recent increases in the levels in fish (International Joint Commission 1983) and say we have failed? We could count the number of people currently working on the problems of toxic chemicals compared with 1978 or look at the chemical analytical capability and say that the situation has improved. Or we could look at the improvements in radiodating sediment cores for retrospective analysis of loadings of chemicals or the pros and cons of herring gulls versus double-crested cormorants as indicators. To judge the effectiveness of the 1978 Agreement, I think, needs something much bigger and more comprehensive.

The purpose of this essay is to see whether the Great Lakes Water Quality Agreement is adequate as a framework for investigation and control of persistent toxic chemicals and to see whether the programs and activities are being carried out effectively.

There is a growing realization that toxic chemicals pose an extremely complex hazard to the Great Lakes. The complexity is derived partly from the following four properties of the chemicals. They are not only toxic and persistent as the Agreement acknowledges, but also are dispersed when released and bioconcentrated in organisms. The complexity is also derived from the "multimedia" pathways that the chemicals follow in entering or moving through the environment. These chemicals can get into the environment by direct aqueous discharge, vaporization in smokestacks, or volatilization and seepage from chemical landfill sites. Once in the environment they can move long distances in water or in the atmosphere and can be precipitated on or evaporate from land and water. Control of one route into the environment may lead to pollution by another route of entry. Finally, they pose serious administrative problems because release into the environment in one jurisdiction can result in transboundary pollution and damage in another jurisdiction.

To understand the complexity of the problems posed by toxic chemicals in the Great Lakes requires special conceptual tools to sort out the most important aspects. I want to juxtapose two rather underutilized concepts. The first is the science of human ecology and the second is the idea of critical pathway analysis as developed for radiation protection. I also want to restrict the geographic extent of the analysis to the Niagara River and Lake Ontario as an example of the inherent complexity and of the kinds of problems posed to administration of the Agreement. Biota from Lake Ontario had the highest levels and the greatest diversity of chemicals of any biota sampled from the jointly administered Great Lakes.

Several reports have been written on pollution of the Niagara River. The New York Public Interest Research Group published (Hang and Salvo 1981) a major study of industrial and municipal effluents and of chemical dump sites in the New York Niagara frontier. Reports written by the Canada–Ontario Review Board (1980, 1981) compared levels from chemical analysis with water quality objectives. The recent report of the Niagara River Toxics Committee (1984) documented the sources of toxic chemicals to the Niagara River, compared levels with water quality objectives, and recommended remedial options. Recent evidence of the long-term loadings of organochlorine chemicals to the Niagara River and Lake Ontario has been derived from an accurately radiodated sediment core (Durham and Oliver 1983). The results showed that there was a progressive increase in contamination since about 1915 with the highest levels contained in sediments laid down in the late 1950s until the early 1970s. Evidence of continuing significant loadings of chemicals to the Niagara River has been provided by statistical analysis of three data sets (El-Shaarawi et al. 1985).

The framework of human ecology can help in understanding the complexity of the problems posed by chemicals discharged to the Niagara River and Lake Ontario. Human ecology is a branch of sociology developed at the University of Chicago during the 1920s and based on the premises that man is a social organism and that populations of man adapt to the environment through technology and social organization (Duncan 1964) and by processing energy, matter, and information (Micklin and Choldin 1984). Boulding (1981) has developed a nine-point heuristic model of human ecology in his book entitled *Ecodynamics: A New Theory of Societal Evolution*. The nine reference points of the model are Populations, Social Organization, Technology, Matter, Energy, Knowledge (Information), Threat Systems, Integration, and Exchange. I want to work through these nine reference points to see some of the components involved in the issue of toxic chemicals and the Niagara River and to see some of the interactions between the components.

Critical pathway analysis, as it has been developed for radiation protection, can be used to focus the discussion on the more important processes. The idea (National Academy of Sciences 1975) is that people are exposed to various nuclides that travel by various routes through the environment after entering the environment from various sources. However, the situation can be simplified because specific groups of people, who are likely to be exposed to elevated levels, can be identified and they are likely to be mainly exposed through only one or two routes. These routes are known as the critical pathways and the specific groups of people are known as critical subpopulations. It should be noted that this is a very different approach from the usual analysis which is concerned with investigations of, or regulatory control to, exposure of substances to the *average* population. Exposures, for the average population, are controlled using toxicological data for risk analysis to set guidelines and tolerances using conservative safety factors. Discharge regulations based on protection of the critical subpopulations are assumed to result in protection of all other populations. The Niagara River is only one of four critical locations on the Great Lakes. The others are the Detroit River, Saginaw Bay, and Green Bay and critical pathway analyses could be prepared for these locations. The general outline of the issues would, however, likely be the same as for the Niagara River.

Critical Subpopulations

Many people living in the Great Lakes basin are exposed to chemicals through a variety of routes but it is important to identify who is likely to be exposed to the highest levels. Two identified critical subpopulations are those groups that live close to chemical landfill sites or work at the chemical manufacturing plants (Levine 1982). Recent work (Vianna and Polan 1984) has shown an association between low birth weight and residence near the Love Canal swales during the period of dumping chemical wastes. One other likely critical pathway to man is through the consumption of large Lake Ontario fish. Although there are no data to substantiate the existence of critical subpopulations, we can postulate that the following are or have been exposed to various quantities of toxic chemicals by this route: (1) Lake Ontario commercial fishermen, their wives, and their families who have regularly eaten parts of their catches of large salmonids during the past 30 yr, (2) Lake Ontario sport fishermen who caught, froze, and ate large salmonids during the past 10 yr, (3) Native groups that may have been heavily dependent on Lake Ontario salmonids during the past 30 yr.

In contrast, other routes of exposure, such as drinking water, bath water, or swimming, appear to be trivial in comparison with the ingestion of fish. Ingestion of 1 kg of fish that contains one part per million (10^{-6}) of a persistent toxic chemical is equivalent to drinking a tonne of water containing one part per billion of the chemical. In reality, organochlorine chemicals are usually not present at more than part per trillion (10^{-12}) concentrations in the raw waters of Lake Ontario.

Annex 12 of the 1978 Great Lakes Water Quality Agreement states:

> Monitoring and research programs should be established to identify the impact of persistent toxic substances on the health of humans.

There are no projects being undertaken to identify the commercial fishermen and their families who may have been chronically exposed, particularly during the period of highest discharges in the 1960s. Preliminary work has been undertaken on sport fishermen by Dr. Ron Sonstegard (MacMaster University, Hamilton, Ont., pers. comm.). With the exception of the research on the St. Regis Reserve, no work has been done to identify native groups or special ethnic groups that are heavily dependent on fish. More particularly, no prospective or retrospective epidemiological work (Lilienfeld 1983) has been undertaken or, to my knowledge, is planned. There is a priority requirement for development of a program to undertake this research because studies of mothers who ate PCB-contaminated fish from Lake Michigan had infants who were 160–190 g lighter and had smaller head circumferences than infants of a non-fish-eating control group (Fein et al. 1984). The infants also showed marked behavioral anomalies (Jacobson et al. 1984). There is a resistance to initiating epidemiological research on a particular population if no effect has been found. However, without a pilot scale epidemiological study it is difficult to find any effects, particularly subtle ones such as increases in abnormalities or other reproductive effects or an elevated incidence of cancer. This catch 22 situation can only be broken by an intuitive individual who is prepared to risk finding nothing.

In addition to the toxicological effects on humans there may be socioeconomic effects on populations. Some preliminary work is being done by Ted Cowan (Department of Fisheries and Oceans, Toronto, Ont., pers. comm.) on the economic impact of chemicals on the Lake Ontario fishery. Without data on the impact of chemicals on human health or socioeconomic well-being, no case can be made that there has been any damage. Without demonstration of damage to health, property, or livelihood there is little impetus for a concerted effort to clean up the sources and no way in which to obtain compensation for those affected.

Before leaving the subject of critical subpopulations it is worth noting that breast-fed infants are likely to be exposed to even higher concentrations than their fish-eating mothers. Because the fetus and newborn infants can be more susceptible to the effects of chemical contaminants than adults (Casarett and Doull 1975), there is a priority requirement to identify and monitor these critically exposed individuals.

We can extend this idea of critical subpopulations from humans to nonhuman organisms. What organisms might be particularly at risk? Remarkably little is known about the effects of releases of toxic chemicals to the Niagara River on nonhuman mammals. In Michigan and southwest Ontario there were cases of severe reproductive failure in ranch-mink operations about 20 years ago (Hartsough 1965). This was mainly attributed to the presence of PCB in Great Lakes fish which was being used as a feedstuff for the adult mink (Aulerich et al. 1973). There are indications that wild populations of mink and otter close to Lake Ontario have declined (Robert Foley, New York State Department of Environmental Conservation, Gloversville, NY, pers. comm.).

The state of the evidence is considerably better with fish-feeding birds that are critically exposed to chemicals through the food chain. There are not only long-term trend data on levels of organochlorine chemicals (Mineau et al. 1984) in herring gull eggs but also detailed knowledge about the outbreak of chick edema disease that occurred in the late 1960s and early 1970s and that caused severe embryonic abnormalities and mortality (Gilbertson 1983). There is a new outbreak of this disease in fish-feeding birds in Green Bay, Lake Michigan (Tim Kubiak, U.S. Fish and Wildlife Service, Green Bay, WI, pers. comm.). Studies on double-crested cormorants showed severe reproductive failure mainly due to eggshell thinning (Weseloh et al. 1983). Unfortunately, Canada has decided that no more work on such effects will be undertaken, although there are still some fairly gross gaps in our knowledge. For instance, there are no ospreys or bald eagles nesting in the vicinity of Lake Ontario (Gilbertson 1975). When did they disappear and what caused their disappearance? Effects on birds and mammals were noted at least a decade before work was initiated on humans. There was, however, a very tenuous link between these groups of researchers, and the bizarre findings from the bird work were unable to stimulate research on humans.

There are reliable long-term trend data now available on levels of chemicals in fish (International Joint Commission 1983). There are also some epidemiological studies on the incidence of tumors in fish (Leatherland and Sonstegard 1984). Information on how the presence of tumors might be related to chemicals is missing except for lip papillomas in brown bullhead (*Ictalurus nebulosus*) (Black 1983). What are the fish species that are or were critically exposed to chemicals? There are many changes (Great Lakes Fishery Commission 1979) that have occurred in Lake Ontario fish populations during the past 30 yr when peak loadings of organochlorine compounds occurred (Durham and Oliver 1983). Were any of these changes

caused by chemicals or was it eutrophication or abuses of harvesting? The debate goes on. However, fisheries biologists and managers could only observe this massive deterioration of the fishery but were at a loss to attribute, reliably and unequivocally, what they observed to a causal agent or series of causal agents. Probably all the agents caused the changes and only a multifactorial explanation will, in the end, prove satisfactory (Kuchenberg 1978).

Are there likely to be critical subpopulations of benthic invertebrates, zooplankton, or phytoplankton? Where are they likely to be found? Do toxic chemicals from the Niagara River affect their productivity? Preliminary evidence (Dr. R. Thomas, International Joint Commission, Windsor, pers. comm.) indicates that the Niagara River has a significant effect on nanoplankton production in Lake Ontario. There are also indications that the increased incidence of deformities in populations of chironomid larvae may be related to recent exposures to contaminants (Warwick 1980). The 1978 Great Lakes Water Quality Agreement states that monitoring and research programs should be established at a level sufficient to identify the impact of persistent toxic substances on the quality and health of living aquatic systems. I am not sure that we have yet satisfactorily addressed the topic of impact on aquatic organisms. I am not referring to determination of the levels of chemicals in organisms but to demonstrating whether deleterious biological effects are occurring in the field.

Social Organization

People band into groups and organize for particular purposes. What are the critical organizations involved in the issues of toxic chemicals on the Niagara River? The primary concerns are the chemical manufacturing industries that produce the chemicals. These include the former Hooker Chemicals and Plastics Corporation which has now been taken over by Occidental Chemical Corporation.

Because the chemicals have posed dangers to human health and the environment, various levels of government have become involved: these include New York State Department of Environmental Conservation and the Department of Health, U.S. Environmental Protection Agency, Environment Canada, Department of Fisheries and Oceans, and the Ontario Ministry of Environment and Ministry of Natural Resources. These bilateral international as well as federal/state and federal/provincial involvements pose problems of jurisdictional responsibility. In addition, they pose a dilemma for intergovernmental relations. How can the Canadian Government reconcile its policy of improvement of Canada – U.S. relations with the suspected or actual damage to property and health caused by transboundary pollution in contravention of Article IV of the International Boundary Waters Treaty of 1909? How will the recent landslide victories in both Canada and the United States affect environmental programs for research and cleanup on the Great Lakes?

Many of these government organizations have been remarkably slow to comprehend the situation and none understood the situation when it was most severe in the 1960s. These organizations have been staffed by rather conventional scientists undertaking "normal science," that is, elaborating the existing body of knowledge. Very few scientists have been allowed to undertake "real science" by looking for anomalies and forming testable hypotheses based on those observations of anomalies (Kuhn 1970). There has also been an emphasis on sophisticated capital equipment rather than on imagination, creativity, and intuitive curiosity. In an historical context most personnel in the various governments have been remarkably ineffective in recognizing toxic chemicals problems in a timely manner. In retrospect, the relative priority accorded the eutrophication problem during the late 1960s and early 1970s was likely unwarranted given the actual, but unperceived severity of the toxic chemicals problems occurring at that time. There is a priority requirement for government research organizations to maintain a small group of personnel dedicated to finding new problems free from the pressures imposed by the system to publish to demonstrate merit. The "Early Warning System" outlined in Annex 12 of the Agreement is a litany of "late warning" conventionality. If this had been followed in the early 1970s none of the research on fish-feeding birds or fish tumors would have been initiated. There is a need to include searching for new biological anomalies, in the field, such as reproductive failure, abnormalities, and tumors or changes in growth, mortality, or physiology and biochemistry of organisms.

I want briefly to identify a few other organizations that have been key players in the effectiveness or otherwise of the resolution of the problems posed by toxic chemicals entering the Niagara River. Much of the initiative for cleanup, compensation, or protection of health relative to transboundary pollution has come from public interest groups such as the Love Canal Homeowners' Association, Pollution Probe, Operation Clean – Niagara and the Ecumenical Task Force. The Great Lakes Fishery Commission and the Ontario Council of Commercial Fishermen have been faced with a difficult dilemma. Should they become receptive to the message about the reality of contaminants or should they discourage discussion of the information so that short-term interests are not jeopardized? Recently, these organizations have become interested in the problems posed by chemicals and in their early resolution so that a viable fishery can be reestablished. Their interest and possible political involvement could lend significant impetus to cleaning up the chemical waste landfills and effluent discharges because fishermen's livelihoods and health are most directly at risk because of chemical contamination. The International Joint Commission is potentially an important forum for settling Canada – United States bilateral issues if the two countries choose to use it for this purpose.

Technology, Energy, and Matter

Human ecology can also help in trying to understand why the application of the technology for the chlorine chemical industry should have caused such severe problems near one of the world's most spectacular waterfalls. Niagara Falls of course is an enormous source of energy that can be translated into electric power through turbine generators. Chemical industries are concerned with the transformation of matter, and particularly large amounts of electric energy are needed by the chlorine chemical industry. Thus it was natural that this kind of industry would locate at Niagara Falls. The saleable outputs from these plants were chlorine, caustic soda, caustic potash, and related inorganic compounds. In addition, in 1915, Hooker Electrochemical Company began operation of its first chlorobenzene plant in the United States with a capacity of 8200 tonnes (t) per year (Kirk-Othmer 1979). Later, when the technology for production of other organochlorine compounds became available, a wide array of pesticides, plastics, and flame retardants and other chemical products was produced. There were also, however, organochlorine compounds produced as inadvertent by-products

when the electrochemical industry started, and these can still be detected in the historical sequence preserved in the sediments of Lake Ontario (Durham and Oliver 1983). Besides the aqueous discharges of organochlorine by-products, there were chemical wastes deposited in landfill sites or discharged to the atmosphere. Information about the identity and quantities of chemicals released or deposited in these various ways and about their pathways of translocation by groundwater, atmospheric air masses, and other hydrologic processes is still sketchy although litigation proceedings have enabled the provision of some data.

In retrospect, we should ask whether this kind of chemical manufacturing technology is appropriate for this kind of location. Is it, in fact, so dangerous and uncontrollable that, as in the case of kepone production by Life Sciences Inc. at Hopewell, Virginia, on the James River and consequent pollution of Chesapeake Bay, it should be totally proscribed and the manufacturers treated as criminals? With more and more revelations, through the United States litigation proceedings, it is becoming apparent that not only is the technology inappropriate for such a location but also the housekeeping practices employed by the chemical companies were woefully inadequate to protect Lake Ontario from becoming one of the most contaminated environments in the world.

There has, however, been a feedback loop from energy availability for the transformation of matter, using increasingly sophisticated organic and inorganic chemical technology, to the increase in population. Even a cursory reading of the history of the Love Canal situation reveals the pressures on the Niagara Falls, New York, Board of Education to find land for building schools for the burgeoning postwar population attracted to the City of Niagara Falls by jobs and the prospect of economic stability. Can we proscribe a significant part of the technology and livelihood that brought this population into existence, particularly if upper New York State is a depressed area? The chemical products of this technology clearly set up an ecologically antagonistic relationship between this population and the population involved in the Lake Ontario fishery.

The Love Canal has become another area where new technology has had to be developed and applied. Canadian engineering consultants, Conestoga Rovers, assessed the site and the fluxes of chemicals from the old canal to the adjacent houses and devised and implemented a rehabilitation plan using a seepage collection system, carbon filtration, and replacement of the impervious clay cap. At the Royal Military College in Kingston, Ont., the effectiveness of a mobile waste-destruction facility, using plasma arc technology, is being tested and if successful may be put into operation for disposal of non-aqueous-phase liquids at the Love Canal. To a large degree, technical solutions for the problems of hazardous chemical waste disposal have been successfully developed. Much the largest problem now is to overcome the community resistance to proposals for siting of disposal facilities.

Love Canal may have become the most notorious chemical dump site in the area but other nearby locations pose even more severe problems. It is estimated that the Hyde Park dump contains 2 t of 2,3,7,8-tetrachlorodibenzo-*p*-dioxin. About 1 kg of this chemical was released by a chemical explosion at Seveso in Italy in 1976 and caused a severe outbreak of chloracne among the local inhabitants. Even now it is uncertain whether there were effects on reproduction or the incidence of cancer; however, the town of Seveso was evacuated and community life was completely dislocated. It is known that this compound is leaching from the Hyde Park and various other dumpsites into the Niagara River but it is uncertain how much has so far entered Lake Ontario from the landfill sites or from other discharges. But it has been found in food chains and was likely a major cause of the reproductive failure and incidence of abnormalities in fish-eating birds in the late 1960s and early 1970s (Gilbertson 1983). The New York Public Interest Research Group (Hang and Salvo 1981) revealed the extent of the landfill sites in the Niagara Falls area. The recent report of the Niagara River Toxics Committee (1984) revealed more than 150 sites within 3 mi of the Niagara River. Twenty-eight sites, including the Hyde Park dump, were shown to be leaking organochlorine chemicals or other persistent toxic chemicals into the river.

The various proceedings in U.S. District Court have shown the enormous technical and financial difficulties involved in cleanup. The Canadian Environment Law Association obtained *amicus curiae* standing in the Hyde Park hearings and represented Pollution Probe and Operation Clean-Niagara. Important points have come out of the settlement agreement (Vigod 1982) on the Hyde Park landfill site. There is a flexible settlement based on "requisite remedial technology." This is not actually defined but the goal of the settlement is to protect against endangerment to human health and the environment in the Hyde Park – Bloody Run area. By applying the critical pathway analysis to this goal it is clear that it is not intended to protect the critical subpopulations outside of the Hyde Park – Bloody Run area. Thus commercial fishermen and their families on the Isle of Quinte or Quebec eel fishermen on the St. Lawrence River apparently remain outside the intent of the settlement. In addition, the goal does not conform to the intent of Annex 12 of the 1978 Great Lakes Water Quality Agreement which states (emphasis added):

> 2. *General Principles*.
> (a) Regulatory strategies for controlling or preventing the input of persistent toxic substances to the Great Lakes System shall be adopted in accordance with the following principles:
> (i) The intent of programs specified in this Annex is to *virtually eliminate* the input of persistent toxic substances in order to protect human health and to ensure the continued health and productivity of living aquatic resources and man's use thereof;
> (ii) The philosophy adopted for control of inputs of persistent toxic substances shall be *zero discharge*.
> (b) The Parties shall take all reasonable and practical measures to rehabilitate those portions of the Great Lakes System adversely affected by persistent toxic substances.

Annex 12 of the Agreement could have been made much more specific by development of an Annex containing the names of "persistent toxic substances" that the two Parties agreed should be "eliminated" as sources. The release of these chemicals could then have been proscribed by treaty. The following is a short list of persistent toxic substances that should be subject to the provisions of Annex 12 and on which bilateral agreement could possibly be attained at an early date:

Aldrin/dieldrin
Chlordane and related compounds
DDT and metabolites
Endrin
Hexachlorobenzene and hexachlorobutadiene
Heptachlor/heptachlor epoxide
Hexachlorocyclohexane
Kepone

Mirex and related dechloranes and impurities
Toxaphene and related impurities and isomers
Polychlorinated biphenyls
Polychlorinated terphenyls
Polybrominated biphenyls
2,3,7,8-Tetrachlorodibenzo-*p*-dioxin

An executive of the U.S. Environmental Protection Agency recently stated that to dig up the Hyde Park site and dispose of the chemical wastes so as to "eliminate" the input of persistent toxic substances would likely bankrupt Occidental Chemical Corporation, which is the 18th largest American corporation. The U.S. Environmental Protection Agency, in negotiations of the interpretation of requisite remedial technology, have requested Occidental to undertake a study of the benefits that might be derived from cleanup of the various sites for which it is responsible. Some of the critical groups outside the immediate Hyde Park – Bloody Run area might be included in that study (Murray Brooksbank, Environmental Protection Service, Toronto, Ont., pers. comm.). Canada is in a serious dilemma to know what it can reasonably expect the United States to do so that the problem of toxic chemicals in Lake Ontario does not persist well into the next century. On the other hand, excessive pressure might alienate our powerful neighbour and ally.

Not only does the goal of the settlement not conform to the intent of Annex 12, but Annex 1, which sets out specific water quality objectives for the Great Lakes, also apparently conflicts with this intent. This has been pointed out by the United States members of the Niagara River Toxics Committee (1984) in their statement of position on Recommendations 23 and 24 concerning an overall allocation plan and the philosophy of zero discharge. By setting water quality objectives for organochlorine compounds that are persistent, toxic, widely dispersed, and bioaccumulated, the two Parties have implicitly accepted the discharge of these compounds to the waters of the Great Lakes and their interconnecting channels.

Much of the rationale and history of water quality objectives can be found in McKee and Wolf (1963). In their introduction they stated (emphasis added) that:

> The formulation of waste-discharge requirements should be so designed as to (1) secure that degree of care in the planning and operation of works for the treatment and disposal of sewage and industrial wastes as will adequately protect the public health and the beneficial uses of waters of the State and (2) at the same time permit the legitimate planned usage of those waters for receiving *suitably prepared* wastes so that an orderly growth and expansion of cities and industries may be possible.

In 1963, water authorities were mostly concerned with treatment of municipal sewage and biodegradable industrial wastes. Despite the chemical crisis that was actually occurring and the publication of *Silent Spring* by Rachel Carson in 1962, concern about persistent toxic substances in industrial wastes was not to arise as a serious political issue in the Great Lakes area until about 15 yr later. The underlying premise on which the above formulation is based is that wastes can be "suitably prepared." Sewage and many organic and inorganic chemical wastes can be "suitably prepared," by biological and chemical treatment, for disposal into receiving waters. Persistent toxic chemicals, however, cannot be treated using conventional wastewater treatment technology; thus, the underlying premise for preparing water quality objectives for this small class of compounds does not hold.

This raises the question again whether these chemicals should be manufactured, because if wastes from their production and disposal cannot be released to water, then their manufacture may be in jeopardy. Again there is a growing public consensus that this small group of chemicals should only be manufactured if there are no aqueous or gaseous discharges from production or disposal. Thus these chemicals should only be produced at industrial sites that include a high-temperature incinerator for complete destruction of wastes.

Past industrial practices, particularly on the Niagara River, have resulted in transboundary pollution, closures of fisheries, wildlife diseases, and exposure of critical subpopulations of humans to potent long-lived teratogenic, carcinogenic, and cocarcinogenic chemicals. The underlying premises for setting water quality objectives for organochlorine persistent toxic substances are, I believe, indefensible. Thus the philosophy of zero discharge and virtual elimination, contained in Annex 12, should be given precedence and the water quality objectives for persistent toxic substances contained in Annex 1 of the Great Lakes Water Quality Agreement of 1978 should be removed. Similarly, the idea contained in paragraph 7(c) of Annex 12 concerning "calculation of acceptable loading rates for persistent toxic substances" is in conflict with paragraph 2. There is only one acceptable loading rate and that is zero. How much is zero? A little less than a part per quadrillion (10^{-15}), which is about the present limit of chemical analytical technology.

Information

One final aspect of technology should be mentioned as it relates to the accumulation of information. During the past decade there has been an improvement of six orders of magnitude in routine chemical analytical techniques. Both the machines and methods of analysis have become more sophisticated. The result is that chemistry has caught up with the "early warning" anomalies observed in biological field studies of effects and, belatedly, enabled an interpretation of such phenomena as chick edema disease (Gilbertson 1983) seen in fish-feeding bird populations in the late 1960s and early 1970s. The great hope is that ultratrace organic chemistry can now detect all the compounds that are of biological significance and that there will not be too many chemical "surprises" in the next decade or so. In this sense the two Parties to the Agreement may have become very effective in developing programs "to identify the presence of previously unidentified persistent toxic substances" (Annex 12.4.d.).

The increased ability to detect and identify chemicals has inevitably resulted in the "list complex." Lists pose a dilemma about how to do research. If a chemist finds a chemical in a human autopsy sample, bird eggs, fish flesh, sediments, or some other environmental material, should the toxicologist follow the chemist and determine the biological significance of the chemical through controlled laboratory experiments? Or, should the field biologist be relied upon to report what is happening biologically in the real world and get the toxicologist and chemist to help test hypotheses that originate from field observations of biological effects? The discovery of mirex hiding beneath a PCB peak was a brilliant piece of chemical analytical sleuthing (Kaiser 1974), but I am not convinced that mirex was of any toxicological significance to the biology of Lake Ontario. Testing for its toxicological properties did, however, divert scarce resources away from the search for the chick edema factor during the late 1970s. To be effective we need to keep our

eyes on the critical compounds. Mirex was likely not a critical compound; 2,3,7,8-tetrachlorodibenzo-*p*-dioxin likely was.

It is worth noting that the research on birds had an amazing power to find problems and to provide testable hypotheses. By 1975, the Canadian Wildlife Service had reported the presence of chick edema disease in fish-feeding birds in Lake Ontario, to the International Joint Commission (1975). There are only a limited number of chick edema active compounds and these include a few of the chlorinated biphenyls, dibenzo-*p*-dioxins, dibenzofurans, azobenzenes, and azoxybenzenes. The bird work, however, was remarkably impotent in galvanizing the international research community to look for these chemicals. In addition, the possible toxicological interactions between these various compounds and their relative contribution to the observed effects should have been investigated. Again, Annex 12 specifically states that research of interaction effects of residues of toxic substances on aquatic life and wildlife should be conducted.

There are some disturbing new data on polychlorinated biphenyl levels from the long-term monitoring of fish (International Joint Commission 1983). Levels in Lake Ontario lake trout (*Salvelinus namaycush*) had been declining significantly during the late 1970s. However, since 1981 the levels have increased by more than 50%. There is, as yet, no adequate explanation for this. Nor is there an explanation of why the levels in Lake Ontario herring gulls should have continued to decline.

Various mass-balance estimates indicate that atmospheric sources of PCB are significant (National Research Council 1984). However, there are also hundreds of tonnes of PCB in the Hyde Park landfill site and the continuing high levels may be in some way interrelated with this. The continuing uncertainties about the relative importance of the sources of organochlorine pollutants and particularly PCB indicate that we have not been very effective in carrying out part 4(c) of Annex 12 of the Agreement which states:

> Monitoring and research programs should be established at a sufficient level to identify the sources of input of persistent toxic chemicals.

Finally, under the information section, I would be remiss not to comment on the cybernetic subsystem (Buckley 1968) which Canada and the United States have in existence to solve problems such as toxic chemical discharges. If we are going to judge effectiveness of the Agreement, we had better have a description of the negative feedback mechanisms. These two countries have opted for what can be called the "Science, Media, and Politics" subsystem. Typically, an invention is applied to enable humans to adapt better to the environment. Subsequently some deleterious effect is recognized which is reported in a scientific publication. The media may then pick up the story and if there is sufficient interest, there may be a public reaction to the situation. With sufficient public reaction, there is likely to be political reaction which will enable bureaucrats to obtain funding to research the deleterious effects in detail. Henry Regier (University of Toronto, pers. comm.) recently stated that, for environmental concerns, this stage was generally not reached in less than 10 yr after the initial application of the technology.

The new funding will be used to document the scope and severity of the phenomenon. Further media, public, and political interest will start demanding a solution and bureaucrats will start negotiating for action. In the United States, this may involve an administrative law judge; in Canada, there will be meetings between the responsible agencies and the industry involved. Finally, some kind of control action will be developed and promulgated, and the effectiveness of the controls may be subsequently measured to evaluate whether the original problem has been solved. It is not uncommon for the full process to involve more than 25 yr (Lawless 1977). As examples, I would cite the case of DDT which was applied on a widespread basis in agriculture about 1945 and largely banned in Canada in 1969 and in the United States in 1973. Similarly, PCB's were manufactured extensively by about 1930, their toxicological properties were noted in the mid-1940s, but they were not initially controlled on an international basis until 1973. National controls were not implemented until 1978 in Canada and about 1979 in the United States. The issue of acid rain is another contemporary case in point.

By any standards, it would seem that this subsystem is inefficient, because irreparable damage, such as the widespread extirpation of the peregrine falcon and severe contamination of Great Lake fisheries stocks, has resulted before controls have been instituted. The American system, however, may not be ineffective because, in the end, all interest groups have been heard and are more likely to assimilate the outcome. Other societies, such as Great Britain, have used a different model that is more efficient in making decisions and saving the peregrine falcon population, although not necessarily as effective in coopting all the interest groups. The British model relies more on decision-making by small committees of scientists, bureaucrats, and representatives of interest groups (Snow 1962). Canada tends to be between these two models with a heavy reliance on media, public, and political pressure, but also tending to make decisions through small committees of experts. The various models reflect the historic developments of the different societies and the degree of heterogeneity of their value systems.

It is worth recording that the Environment Contaminants Bill was given Royal Assent in December 1975 within 3 mo of the Globe and Mail's running a major series of articles questioning the suitability of PCB-contaminated Lake Ontario coho salmon (*Oncorhynchus kisutch*) as food for human consumption. This is a Canadian example of the effectiveness of the science, media, and political subsystem in operation since the Bill had been languishing for about 6 mo at the bottom of the Order Paper after first reading in the House of Commons.

Threat System

The threat system can act in a variety of ways at a variety of levels. Perhaps the most insidious aspect has been the treatment of individual scientists who have found some bad news about a chemical. Levine's book (1982) on the politics of the Love Canal details harassment by New York State of Beverly Paigen, who was investigating the incidence of chromosome damage among Love Canal residents. Part of the vulnerability of the health and environment researchers to these subtle and not so subtle pressures is the lack of strong scientific fraternities or other organizations to which the individuals can turn for support. This is in sharp contrast with the situation for doctors, lawyers, or engineers for instance. Perhaps the lack of strong associations of scientists reflects the implicit competitiveness between researchers.

How does this all relate to effectiveness? If the threats are successful, genuine "early warning" messages may be destroyed

and destruction of the message may delay a perception of the reality of the dangers posed by the chemicals. This in turn may result in delays in implementing controls. This is not a topic with which most scientists feel very comfortable; however, if the Donner Foundation grant is to be used effectively, this aspect of the human ecology of the Niagara River situation should be identified and discussed. Similarly, the possibility of pressures against dissident workers occupationally exposed to chemicals might be explored.

At another level, organizations threaten other organizations and in turn receive threats. For instance, various governments in the United States at the municipal, state, and federal levels have indicted each other and the chemical companies for the past chemical landfill practices that are posing hazards through continued leakage.

At another level, the Department of External Affairs in Canada has sent a series of diplomatic notes informing the U.S. State Department of various research findings such as the presence of dioxins and of Canada's displeasure about the state of the Lake Ontario environment and of the tardiness of the cleanup. The Canadian Government has relied on public interest groups such as Pollution Probe to represent Canadian interests in the United States litigation proceedings over the cleanup of the dump sites. The Province of Ontario became involved in the U.S. District Court proceedings concerning the S-Area dump, after obtaining intervener status. The attempts by Canada to refer the matter of toxic chemicals and the Niagara River to the International Joint Commission may have been perceived, by the United States, as a threat because of Canada's known dissatisfaction with the process of *in camera* consultation through the Niagara River Toxics Committee. Canada, of course, could escalate the threats by taking the unprecedented step of referring the matter unilaterally to the International Joint Commission under Article IX of the Boundary Waters Treaty. In turn, there is a series of scenarios of the actions that the United States could respond with — inluding cooperation, of course. If the two countries were reluctant to use the International Joint Commission to investigate or adjudicate the case, Canada has the option to take the case to the International Court in the Hague. However, use of these institutionalized threat systems is likely to be much less effective than the delicate process of diplomatic negotiation. Although this process will take a long time, Canada must continue to engage in this process because Canada is completely dependent on United States action to clean up these sources of transboundary pollution.

To a large extent, the Niagara River situation has been overshadowed by the acid rain issue which has been the Canadian environmental priority of the early 1980s. Ottawa has been relatively successful in informing Washington of Canadian perceptions of the acid rain situation and the two countries have appointed emissaries to try to resolve the differences. Canada may have to mount a similar media and diplomatic campaign to inform the American public and Congress of the Niagara River issue. To date, Washington has regarded the problems of toxic chemicals on the Niagara River as a local issue rather than as a chronic international irritant. Ottawa has, of course, had to place the Niagara River situation in the context of other Canada – United States bilateral issues such as negotiations on free trade, participation in Star Wars, NATO, and the new DEW line, application of extraterritorial legislation, and joint resource management such as salmon allocation and the Garrison diversion. What priority does the Niagara River warrant compared with these other issues, given that the issues cannot be linked?

New information on the presence and effects of deleterious substances in the environment represents a threat to institutions. There seems to be a fairly stereotyped series of responses to new information about the presence of toxic chemicals in the environment. These stereotyped responses, known as the three-step idea – acceptance syndrome, were referred to in an editorial (Hickey 1970) introducing the edition of the *Canadian Field Naturalist Journal* devoted to the status of the peregrine falcon population in North America. The three-point responses were, firstly, denial: "We do not believe it"; secondly, discounting the significance of the findings: "It is of no importance anyway"; and thirdly, didactic confidence: "We knew it all the time." All three responses are ineffective in attempts to resolve the problems. To a large extent the report of the Niagara River Toxics Committee (1984) and of the Canada–Ontario Review Board (1980, 1981) were exercises in denial of the severity and significance of the toxic chemicals problem on the Niagara River.

Integration

In many ways this aspect of the human ecology model is the most difficult to comprehend. It is the sum total of the threats, approvals, and exchanges that bring about cohesion within an identifiable community or between communities. In reading Levine's sociological account (1982) of the politics of the Love Canal situation, I was immediately struck by the lack of cohesion within the critical community adjacent to the Love Canal prior to the inquiries of Lois Gibbs and the subsequent formation of the Love Canal Homeowners' Association. I was also struck by the characteristics of the ethos of the 1950s including mobility, anonymity, acquisition of a basic standard of living, and industrial and urban development. These characteristics do not make for a strong sense of social ties and cohesion. Thus it was perhaps understandable, although not forgiveable, that the Niagara Falls Board of Education, under the gun to educate the children of the burgeoning population, knowingly bought the land and built a school beside the Love Canal and sold the rest of the land for housing development. Liability for this situation is still the subject of litigation proceedings.

I want to contrast that relatively low level of integration among one critical subpopulation with the cohesion among the commercial fishermen on the Isle of Quinte. Almost all are from families established as fishermen on the Isle for up to a century. Everyone knows everyone else and their business. There is a uniform front against anyone who suggests that the fish are contaminated and should not be caught, eaten, or sold. There are threats against Fish Inspection Officers responsible for enforcing closures (Cam Prince, Fish Inspection Office, Kingston, Ont., pers. comm.). Unfortunately, although there is still a fishery on the Isle of Quinte, the levels of chemicals are unlikely to decrease in some fish species in the foreseeable future and therefore the continuity of the fishery and the stability and cohesion of the group are threatened. At present there are no anthropologists looking at the sociocultural aspects of the effects of chemicals on this and similar critical subpopulations.

Annex 13 of the Great Lakes Water Quality Agreement seems to be silent about assessing the socioeconomic and sociocultural impacts of chemicals on communities. If the Agreement is ever renegotiated, these aspects might be included in the research requirements.

In passing, I should note the problems of trying to integrate the scientific community to produce an agreed plan as to how to

tackle hazards posed by "multimedia" chemicals on the Great Lakes. In the First Biennial Report of the International Joint Commission (1982) the absence of overall management of toxic substances control programs, characterized by fragmented, compartmentalized, and insufficiently coordinated activities, was seen as being responsible for duplication, incomplete coverage, and a limited management capacity to effectively address emerging complex problems. To date there has been too much individualism at the personal, institutional, national, and international levels to bring about a unifying plan. Who commands sufficient knowledge, authority, trust, and respect to overcome these centrifugal forces? Not even the International Joint Commission or its Boards has been endowed with sufficient authority, even though most would agree that it has the other ingredients. The lack of an unified plan, during the past decade, will likely result in an inadequate data base for Occidental Chemical Corporation to prepare a comprehensive benefits study concerning the cleanup of their dump sites.

Exchange

Exchanges bind people, institutions, and countries into reciprocal relationships. How have exchanges been affected by contaminants? If we look at the critical subpopulation of commercial fishermen, it is apparent that there are all sorts of exchanges occurring. Other than exchanges with each other of money and perhaps even presents of contaminated fish, there are important exchanges with government. A commercial fishing license represents an exchange between the provincial government that owns the proprietary rights and the fisherman who pays for access. The fisherman, in turn, catches and sells fish and pays taxes. If these exchanges have occurred and the provincial government and fisherman have bound themselves in a reciprocal relationship, does the government also have a duty to protect the fisherman from the effects of the chemicals on his livelihood and on his health and that of his family?

Chemicals have posed enormous new ethical questions for governments. For instance, should the governments intervene in the sport fishery and native food fishery if it knows that its health advisories are being flagrantly disregarded and that society might have to pay the health costs of those individuals that made conscious and knowing decisions to eat the contaminated fish? Government has intervened in other areas of safety and health such as implementing seat belt legislation and requirements for life jackets on small craft and protective hats on building sites. Besides the economic losses to outfitters, boat, and tackle manufacturers there would also be the loss of a powerful constituency lobbying for pollution controls. Should the Canadian Federal Government become involved in U.S. District Court litigation so that its interests can be represented in the various settlement agreements concerning the disposition of the dump sites?

If at all possible, there has been a tendency to try to keep open fisheries that have been contaminated. There have, however, been some unintended consequences of this action. Certain foreign governments have rightly or wrongly rejected or held up distribution of fish from certain parts of the Great Lakes and St. Lawrence River. Publicity surrounding these actions tends to have produced an unfavorable reaction to all Canadian fisheries produce because foreign consumers may be ignorant of the elementary geography of Canada. Can we continue to jeopardize all Canadian fisheries to ensure the continued existence of the Lake Ontario fishery?

In 1982 a complex multinational situation arose because of discharges of persistent toxic chemicals to the Niagara River from the United States side. Lake Ontario American eel (*Anguilla rostrata*), which had become contaminated with a variety of organochlorine compounds, migrated down the St. Lawrence River and were caught by Quebec fishermen. The eels were certified for export by the Department of Fisheries and Oceans, and a Quebec exporter sent them to the Port of Hamburg in Germany. Authorities at the Port of Hamburg tested the eels and declared them unfit for human consumption because of mirex contamination. The Quebec fishermen were paid at a reduced market price after the German market collapsed. Alternative markets offer about half the price of the former German markets that now insist on strict certification.

Canada and the United States are trading partners. We exchange not only goods and services, but also ambassadors and, occasionally, diplomatic notes protesting transboundary pollution. Most of these exchanges have bound us together as commercial allies in a fantastically successful economic culture. Transboundary pollution threatens to be a chronic bilateral irritant which will tend to undermine the bonds between the two countries.

We have to live together as neighbours with a common border across which many commodities flow. We have sophisticated systems to ensure that people, drugs, armies, livestocks, radiosignals, and all the other paraphernalia of western technological man do not cross the border in an uncontrolled manner. We control chemicals in international commerce but even now have poor systems to control the release of chemicals into water, air, or groundwater that traverse international boundaries. There is a priority need to develop such systems because this is a matter of mutual national security and sovereignty.

In the final analysis, resolution of the situation comes down to value systems, ethics, and priorities. While the sediments in Lake Ontario were laying down the historic record of massive organochlorine contamination, while fish-eating birds exhibited a scale of reproductive failure and abnormalities that was unprecedented, and Love Canal women produced underweight infants, man reached the moon and walked on its surface and returned safely to earth. In retrospect, did we have appropriate allocation of funding? We are all caught in this ecodynamic web. We can understand it, we can try to cheat it, but eventually we have to come to terms with it. The great American conservationist Aldo Leopold (1949) advocated the development of an ethic for the land. He also noted that exchanges between neighbours must be governed by the universal ethic of the golden rule. I have already mentioned the opprobrium that was meted out on the Life Sciences Inc. managers responsible for production of kepone at Hopewell, Virginia. By extension, application of this universal ethic would indicate that the United States and New York State should proceed against its chemical industry as it would against a mythical branch plant operation "Life Sciences (Canada) Inc." that was found to be producing kepone at Niagara-on-the-Lake, Ont.

The United States and Canada each gave up a part of their sovereignty in 1909 by signing a treaty to create a forum, the International Joint Commission, for the investigation and settlement of disputes concerning aspects of water quantity and water quality at the boundary. In a world in which international law is largely in disarray (Wormser 1962), this is an almost unique institution. The issue of toxic chemicals threatens to be a long-term divisive irritant between the two countries (Carroll 1983). The use of the International Joint Commission, by the

two nations, to assist in the implementation of the Great Lakes Water Quality Agreement is potentially a most powerful mechanism for reducing these bilateral tensions and for promoting amity.

This application of the concepts of human ecology and critical pathway analysis to the problems posed by persistent toxic substances discharged to the Niagara River and Lake Ontario has revealed some of the components and labyrinthine interactions of the system and several areas for needed improvement of the Agreement and of its operation. Future generations will look back on this period of development and marvel that we could have caused such devastation with chemicals and have perceived and understood so little at the time it was happening. The Donner Foundation inquiries into the effectiveness of the 1978 Great Lakes Water Quality Agreement are opportunities to influence the two Parties to the Agreement and thereby to affect the future course of this ongoing crisis and to promote international harmony. This inquiry of the Committee of the Royal Society of Canada and the National Research Council is itself an integral part of the human ecology of the Great Lakes as will be the responses of the two Parties to the inquiry report and the future attitudes of the two Parties towards the Great Lakes Water Quality Agreement.

Conclusions

This essay has been prepared to analyse the effectiveness of the 1978 Great Lakes Water Quality Agreement in relation to the investigation and control of persistent toxic substances. Two underutilized concepts, human ecology and critical pathway analysis, are employed to review the present and historic situations relative to Lake Ontario and the Niagara River and compare these with the terms of the Agreement. Application of these concepts indicates that various critical subpopulations, particularly fishermen and their families who eat Lake Ontario fish, have not been sufficiently identified. Epidemiological studies are needed concerning the health of fishermen. Critical subpopulations of nonhuman biota are identified. Despite the terms of the Agreement, little is known about effects on wild mink or on the decline of the bald eagle and osprey populations or about whether fish and invertebrates have been affected. Research in the early 1970s on herring gulls has provided evidence of an outbreak of chick edema disease, studies on double-crested cormorants showed severe eggshell thinning. There has been an overall decline in the levels of organochlorine chemicals in eggs of herring gulls during the past decade but levels in Lake Ontario fish are again increasing. Mass-balances to identify the sources of the increases are still too crude for effective decision-making. It is still uncertain whether the presence of toxic chemicals in fish has caused any toxicological effects on fish or fish reproduction. There is a need to reevaluate the "Early Warning System" in Annex 12 to include searching for biological anomalies that had been previously undetected in the field. Before the 1974 outbreak of chick edema disease in Lake Ontario herring gulls can be explained, research on the interactive effects of chemicals needs to be undertaken.

The analysis identifies some of the social organizations involved in the issue including industry, governments, commissions, and public and commercial interest groups. Some of these organizations have tried to minimize the contaminants issue because it threatened their short-term interests.

There is a reluctance to implement the "zero discharge" philosophy contained in Annex 12. A U.S. District Court settlement based on "requisite remedial technology" applied to the Hyde Park dumpsite is not designed to protect critical subpopulations outside the immediate area. In addition, the existence of water quality objectives in Annex 1 conflicts with Annex 12 by implicitly accepting the release of persistent toxic substances. A draft list of persistent toxic chemicals that should be subject to the "zero discharge" philosophy is suggested. For these chemicals there is no "acceptable loading rate": discharges for these chemicals must be "eliminated."

A cybernetic subsystem is described that includes science, media, and political components and the effectiveness and efficiency of this and alternate subsystems is discussed.

Scientists who find adverse effects of chemicals pose a threat to various interest groups and are in turn likely to be subject to subtle threats by those interest groups. This, however, does not enable the science, media, and politics subsystem to work efficiently. Various suits and countersuits have been launched between various governments in the United States and the chemical industries involved. At the international level, diplomatic notes have been exchanged concerning various aspects of transboundary pollution posed by persistent toxic substances.

The relative cohesion of various critical subpopulations is noted and the need for an assessment of the socioeconomic and sociocultural impact in these groups is suggested. The consequences of the absence of an unified plan to investigate and control toxic chemicals are noted.

Persistent toxic chemicals discharged to the Niagara River and Lake Ontario pose new problems of ethics, values, and priorities between individuals and social organizations. The International Joint Commission is a unique forum in which to settle international disputes such as the issues posed by continuing transboundary pollution with persistent toxic substances.

It is concluded that, although the Agreement is a comprehensive bilateral arrangement, there are certain aspects that need to be clarified and revised. In addition, there are several programs and activities pursuant to the implementation of the Agreement that need to be developed.

Recommendations

(1) Lake Ontario fish are a potential critical route of exposure of humans to high levels of a variety of toxic organochlorine chemicals. These chemicals have caused subtle reproductive effects on critical subpopulations of fish eaters within the Great Lakes basin. The Agreement states that governments should establish monitoring and research programs to identify the impact of persistent toxic substances on the health of humans. It is recommended that the two Parties to the Agreement undertake preliminary epidemiological studies to determine whether critical subpopulations, that have eaten Lake Ontario fish over a long period of time, exhibit signs of the effects of organochlorine chemicals.

(2) There are also critical subpopulations of nonhuman organisms such as fish, birds, mink, and otter. Case histories are now available linking organochlorine chemicals to reproductive failure of colonial fish-feeding birds nesting on Lake Ontario islands. Chemicals are implicated in the anomalous incidence of tumors in Lake Ontario fish. However, the relative contribution of specific compounds and the interactive effects of pollutants and microbiological agents in the etiology of the diseases have not been investigated. The Agreement states that monitoring and research should be established at a sufficient level to identify the impact and interactions of toxic substances on the

quality and health of living aquatic systems. It is recommended that the two Parties encourage the development of epidemiological approaches to detect whether anomalous effects are occurring in nonhuman organisms exposed to chemicals in the Great Lakes basin. It is recommended that laboratory aquatic toxicology should become oriented toward research on the etiology, including interactions, of biological anomalies observed in the field.

(3) Annex 12 of the Agreement states that the control of discharges of persistent toxic substances should be subject to the philosophy of virtual elimination and zero discharge. It is recommended that the Parties to the Agreement explore the ways in which Annex 12 can be implemented and develop a list of persistent toxic substances that they agree should be subject to these provisions.

(4) In the U.S. District Court proceedings concerning the disposition of the Hyde Park chemical dumpsite, the settlement agreement contained the phrase "requisite remedial technology" to protect against endangerment to human health and the environment in the Hyde Park – Bloody Run area. Requisite remedial technology does not conform to the intent of Annex 12 of the Agreement to virtually eliminate the release of persistent toxic substances. In addition, it does not address the hazards posed to critical subpopulations outside the immediate vicinity of the dumpsite. It is recommended that settlement agreements concerning disposition of hazardous waste dumpsites that have implications for transboundary pollution should incorporate the philosophy of virtual elimination and zero discharge of persistent toxic chemical releases.

(5) There is a need to resolve the conflict between Annex 12 of the Agreement which sets out the principles of virtual elimination and zero discharge of persistent toxic substances and Annex 1 which contains water quality objectives for persistent toxic substances and thus accepts discharges of these chemicals. Water quality objectives have been used to downplay the significance of discharges of persistent toxic chemicals and the seriousness of the situation. It is recommended that the apparent conflict between Annex 1 and Annex 12 of the Agreement be clarified by the Parties to the Agreement.

(6) The occurrence of organochlorine chemicals in Lake Ontario fish poses not only a danger to the health of fish eaters but also the potential for socioeconomic and cultural impacts on various communities. The Agreement does not include any mention that the Parties will undertake studies on these aspects of contaminants. It is recommended that any review of the Agreement should include consideration of the need for study of socioeconomic and cultural impacts of persistent toxic substances.

(7) Persistent toxic chemicals are likely to remain a chronic divisive issue in bilateral relations between the United States and Canada, perhaps even into the next century. The two countries set up a unique forum in 1909, the International Joint Commission, to study, recommend, and even adjudicate matters of difference. It is recommended that the issue of toxic chemical discharges to the Niagara River should be referred to the International Joint Commission to expedite the effective resolution of this issue.

(8) Finally, it seems that the 1978 Great Lakes Water Quality Agreement is a remarkably comprehensive document that addresses most of the managerial and policy issues posed by persistent toxic chemicals that enter the Great Lakes. As has been noted, there is a need to include provisions for undertaking studies of the socioeconomic and cultural implications of chemical contamination on communities. While the Agreement seems to be basically sound, there are many areas of its implementation that require development or improvement as noted in the above recommendations. By opening up the Agreement for review and possible renewal the Parties must be mindful that, although they may gain better defined directions and responsibilities, they also risk losing some of the existing powerful provisions.

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ANNOUNCEMENTS/AVIS

Applied Ocean Acoustics

Halifax, N.S., January 14–16, 1986

The Continuing Education Division of the Technical University of Nova Scotia is planning a seminar entitled "Applied Ocean Acoustics" to be held January 14–16, 1986, in Halifax, Nova Scotia.

For further information, contact Hira N. Ahuja, Technical University of Nova Scotia, P.O. Box 1000, Halifax, N.S. B3J 2X4. Telephone: (902) 429-8300, ext. 364.

L'acoustique en milieu océanique

Halifax (N.-É.), du 14 au 16 janvier 1986

Le département d'éducation permanente de la Technical University of Nova Scotia prévoit tenir un colloque sur l'acoustique en milieu océanique entre le 14 et le 16 janvier à Halifax (Nouvelle-Écosse).

Pour en savoir plus long, veuillez vous adresser à Hira N. Ahuja, Technical University of Nova Scotia, C.P. 1000, Halifax (N.-É.) B3J 2X4. Téléphone : (902) 429-8300, poste 364.

Aquatic Toxicity Workshop

The Twelfth Annual Aquatic Toxicity Workshop will be held in Thunder Bay, Ontario, November 5–8, 1985. The Workshop will include a field trip to the Environmental Research Laboratory in Duluth, Minnesota. The suggested theme of the Workshop is Laboratory-to-Field Extrapolation Technology or utilizing laboratory-derived data to protect the real world ecosystems from pollution effects.

For additional information please contact George Ozburn, Department of Biology, Lakehead University, Thunder Bay, Ont. P7B 5E1, telephone (807) 345-2121, or J. Howard McCormick, Environmental Protection Agency, Duluth, MN 55804, USA, telephone (218) 727-6692.

Atelier sur la toxicité du milieu aquatique

Le douzième atelier annuel sur la toxicité du milieu aquatique aura lieu à Thunder Bay (Ontario), du 5 au 8 novembre 1985. L'atelier comprendra une visite du Laboratoire de recherches environnementales de Duluth (Minnesota). Le thème proposé pour l'atelier est le suivant : Techniques d'extrapolation du laboratoire au milieu réel ou utilisation des résultats de laboratoire pour la protection des écosystèmes du milieu réel contre les effets de la pollution.

Pour de plus amples renseignements, veuillez communiquer avec les personnes suivantes : George Ozburn, Département de biologie, Université Lakehead, Thunder Bay (Ont.) P7B 5E1, téléphone (807) 345-2121, ou J. Howard McCormick, Environmental Protection Agency, Duluth (MN) 55804, É.-U., téléphone (218) 727-6692.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Identification of sockeye salmon (*Oncorhynchus nerka*) stocks in the Stikine River based on egg size measurements **P. C. Craig**

Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*) **J. C. Abbott and L. M. Dill**

Partitioning light attenuation in an acidic lake **S. W. Effler, G. C. Schafran, and C. T. Driscoll**

Stable carbon and nitrogen isotope tracers of trophic dynamics in natural populations and fisheries of the Lahontan Lake system, Nevada **M. L. F. Estep and S. Vigg**

Prey selection by freshwater predators with different foraging strategies **S. D. Cooper, D. W. Smith, and J. R. Bence**

Growth and production of *Eogammarus confervicolus* (Amphipoda: Anisogammaridae) at a log storage site and in areas of undisturbed habitat within the Squamish estuary, British Columbia **M. J. Stanhope and C. D. Levings**

Aluminum bioaccumulation and toxicity to *Daphnia magna* in soft water at low pH **M. Havas**

Inter- and intra-specific variability in the response of zooplankton to acid stress **E. E. Price and M. C. Swift**

Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia **T. D. Beacham and C. B. Murray**

Equilibrium yields and yield isopleths from a general age-structured model of harvested populations **T. A. Lawson and R. Hilborn**

Fish hepatocytes: a model metabolic system **T. W. Moon, P. J. Walsh, and T. P. Mommsen**

Selenium requirement of a bloom-forming planktonic alga from softwater and acidified lakes **J. D. Wehr and L. M. Brown**

Spring meltwater mixing in small arctic lakes **M. A. Bergmann and H. E. Welch**

Annulus development on the second dorsal spine of the spiny dogfish (*Squalus acanthias*) and its validity for age determination **R. J. Beamish and G. A. McFarlane**

Optimizing sampling design for herring spawn surveys in the Strait of Georgia, B.C. **J. F. Schweigert, C. W. Haegele, and M. Stocker**

Suitability of vertical slot and Denil fishways for passing north-temperate, nonsalmonid fish **K. Schwalme, W. C. Mackay, and D. Lindner**

Distinguishing between one-day-old cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) eggs by gas chromatography and SIMCA pattern recognition **H. Knutsen, E. Moksness, and N. B. Vogt**

Seasonal patterns in lipid content of Lake Michigan macroinvertebrates **W. S. Gardner, T. F. Nalepa, W. A. Frez, E. A. Cichocki, and P. F. Landrum**

Notes

Simplified calculation of optimum spawning stock size from Ricker's stock recruitment curve **R. Hilborn**

Use of visual census for estimating population size in northern pike (*Esox lucius*) **L. J. Turner and W. C. Mackay**

Perspectives

Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation? **K. T. Frank and W. C. Leggett**

Obituary/Nécrologie

Henry Benedict Hachey, 1901–1985 **N. J. Campbell**

Book reviews/Comptes rendus

Fishes of the north-eastern Atlantic and the Mediterranean/Poissons de l'Atlantique nord-est et de la Méditerrannée (edited by P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese) **D. E. McAllister and B. W. Coad**

Books received/Livres reçus

Announcements/Avis

JOURNAL OF COASTAL RESEARCH

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This quarterly research journal features professional reports, technical communications, state-of-the-art reviews, reports of meetings, news from the societies, new citations in coastal topics, and book reviews. The 17 x 25 cm perfect-bound format incorporates 120 to 144 pages with color inserts. This journal, which provides a forum for the exchange of ideas on an interdisciplinary basis, is geared for researchers interested in coastal oceanography, geomorphology, geology, biology, ecology, marine climatology, environmental (resource) management, coastal engineering, and remote sensing.

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